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The Effect of Fire Disturbance Level on Plant Re-establishment in Elk Island National Park, Alberta

by

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A THESIS

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Date SEP 18 1981

Abstract

A study was carried out to determine the effects of prescribed burning on two species of understory shrubs in Elk Island National Park, Alberta. The two primary objectives were: 1) to determine the effect of various levels of fire disturbance on plant re-establishment, and 2) to identify and quantify the relative importance of different regenerative mechanisms used by plants in post-fire re-establishment. A secondary objective was to fully document the fuel complex on the burn site.

The effects of fire disturbance level on plant re-establishment were tested on fifty plots located throughout a prescribed burn area in Elk Island National Park. Five levels of fire disturbance were achieved by varying the fuel loadings on each plot. The fuel loadings tested were: 0, 0.17, 0.87, 3.94 and 9.65 kg/m^2. Beaked hazelnut (Corylus cornuta) was the primary target plant; wild red raspberry (Rubus strigosus) occurred on approximately half of the plots and was also investigated. Two methods were used to estimate the effects of burning on plant re-establishment: 1) the presence of live plant tissue was determined by applying orthotolidine and hydrogen peroxide to the stems of the burned plants, and 2) the rate of plant recovery following the fire was determined by measuring the number of sprouts produced on each plot, the

height growth of each sprout, and the number of leaves produced by each sprout. In addition, the target plant above-ground biomass was measured 15 months following the fire by harvesting and weighing the target plants on each plot.

A greenhouse bioassay study was carried out to identify important post-fire regenerative mechanisms. Paired duff cores were removed from each of the 50 plots, one before and one after the fire. The cores were placed in the greenhouse, and the emerging plants were identified and classified as to method of re-establishment - seed or vegetative.

The orthotolidine test indicated that the above-ground portion of all plants experienced at least some fire-induced mortality. Plants on the fuel-free plots were not completely killed, but portions of these plants were exposed to lethal temperatures, presumably through radiation and convective heat transfer from adjacent fuel. All above-ground stems on plots with fuel added were killed. Below-ground portions of plants were killed on seven of the 50 plots, but this mortality was limited to plots with heavier fuel loadings (3.94 and 9.65 kg/m^2). Below-ground mortality on these plots extended 1-3 cm below the surface of the duff. Plants on the remaining plots experienced no below-ground mortality.

The recovery rate data were analyzed using one-way analysis of variance and subsequent multiple comparison tests. Results of this analysis indicated that height growth and the number of leaves were often significantly greater on

the fuel-free plots when compared to the plots on which fuel was added. Significant differences between the fuel-added treatments were few. However, the apparent increase in height growth on the fuel-free plots may have been due to faulty measurement techniques. The number of sprouts was not significantly different between any of the fire disturbance treatments.

The post burn shrub above-ground biomass was analysed using one-way analysis of variance. Hazel biomass was significantly greater on the fuel-free plots. Raspberry biomass was not significantly different between treatments.

A total of 35 plant species were identified on the 100 burned and unburned duff cores placed in the greenhouse. Of these, 13 species reproduced exclusively from seed, 12 resprouted, and 10 utilized some combination of the two methods. Seven species were more common on the unburned cores, while two species were more common on the burned cores. The remaining species were equally represented on the burned and unburned cores.

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1. INTRODUCTION

1.1 General

Fire has long been an agent of disturbance in the boreal forest. The historical presence and frequency of fire occurrence has been well documented (Rowe and Scotter 1973, Kelsall et al. 1977). Records indicate that large fires have frequently occurred in this region; most habitat types which occur in the boreal forest are capable of supporting wildfire under extreme fire weather conditions (VanWagner 1979). Lightning was the principal source of ignition for these fires, although some may have been set deliberately by native inhabitants (Kelsall et al. 1977)

The effects of disturbance by fire on animal and plant communities are an important aspect of the role of fire in the boreal forest. The impact of fire on plants is determined by several factors. They include the physiological and morphological condition of the plant (Wright 1970), the level of fire disturbance experienced by the plant (Stahelin 1943, Komarek 1971), the reproductive mechanisms utilized by the plant (Ahlgren 1960, Noble and Slatyer 1977, Cattelino et al. 1979, Rowe 1979), and the environmental conditions present following the fire (Brown and Davis 1973). In addition, fire has more wide-spread effects on a site by consuming biomass, changing species

composition, and affecting nutrient cycling (Lutz 1956, Ahlgren and Ahlgren 1960, Heinselman 1973). Areas affected by fires may be very large, and in the boreal north, where biological processes are slow, effects of fires may persist for many years (Kelsall et al. 1977).

Effective management of wildland resources in the boreal forest must take into account the specific effects of fire. Knowledge of these effects will assist in further understanding the historic influence of fire, the effects of burning on existing plant communities, and enable the wise application of fire as a cultural tool in managing boreal ecosystems.

1.2 Problem

Elk Island National Park, in east-central Alberta, has historically been subjected to periodic burning. Prairie grass fires were common in the area in presettlement times, and were easily carried from the grasslands into the forested areas during dry months. The historical presence of frequent disturbance by fire has encouraged the introduction of prescribed burning as a cultural tool in park management.

Elk Island National Park management staff began a preliminary burning program in 1979 (Dube 1979), and are presently planning a ten year burning program. The purpose of the burning program is to increase species diversity and to control shrub encroachment onto valuable grazing reserves

(Dube 1979). In addition, some experimental burning is being done to investigate the effects of fire on wildlife forage. A portion of the park was burned in the present study as a part of the experimental wildlife burning program.

Plant response to burning in Elk Island National Park is poorly understood. Little burning has been done to date, and post-fire vegetation monitoring has not been carried out. There have been no major wildfires in the park since its inception as an elk preserve in 1906 (Kjorlien 1977), providing no opportunities for fire effects studies. Further knowledge and understanding of the autecological effects of fire will enable the wildland manager to better utilize prescribed fire to achieve specific management objectives. Therefore, the present study was established to investigate some of the specific effects of prescribed burning on important understory species in the park.

1.3 Study Design

Fire disturbance level is an important factor in determining the response of plants to burning (Woodard 1977). The importance of this factor is widely recognised, but fire disturbance level has seldom been documented under field burning conditions. In addition, fire disturbance level has rarely been experimentally varied under controlled conditions.

In this study, two frequently occurring shrub species indigenous to the burn site were subjected to a range of fire disturbance levels. Disturbance levels were calculated using total heat release (Albini 1976). This quantity is the product of the heat of combustion of the fuel and the weight of fuel consumed. By assuming that heats of combustion do not vary significantly between fuelbeds, total heat release can be regulated by changing the fuel loading. Knowledge of thermal regimes that are lethal to specific plant species will enable the wildland manager to better determine the effect that prescribed burning will have on important plant species.

Fire disturbance level is not the only factor that determines a plant's response to burning. The regenerative mechanisms utilized by the plant also determine whether and to what extent a plant will re-establish following burning. The two mechanisms investigated in this study were vegetative resprouting (Flinn and Wein 1977) and seed buried in the soil (Moore and Wein 1977). Duff cores were removed prior to and subsequent to burning and transported to the greenhouse. Germinated seeds and emerging sprouts were identified and counted. This indicated the relative importance of the two regenerative mechanisms, and allowed an assessment of the effect of burning on subsequent regeneration.

Aspen stands, due to their relatively non-commercial status, have not received intensive study by fire

scientists. In particular, fuels in boreal aspen stands have not been well documented. In an attempt to increase our understanding of the role of various fuel components in aspen stands, a secondary objective of this study was to document the fuel complex on the burn area. The weight and moisture content of the roundwood, grass, litter and duff fuels were measured on the burn area. In addition, a study was carried out to determine the relationship between the depth and weight of the forest floor (F and H layers).

All plant nomenclature in this study follows Moss (1959), except where authorities are given. Ungulate nomenclature is from Soper (1964).

1.4 Objectives

The primary objectives of this study were to:

1. Examine the response of selected target plants over a range of controlled fire disturbance levels, and
2. Identify and quantify the relative importance of the regenerative mechanisms utilized in the post-fire re-establishment of plants occurring on the burn area.
3. A secondary objective of this study was to fully document the fuel complex on the burn area.

1.5 Hypotheses Tested

In order to achieve the stated objectives, two hypotheses were formulated:

1. Increased levels of fire disturbance will result in decreased levels of plant re-establishment.
2. The regenerative mechanisms utilized by a plant species determine its ability to survive a fire and to re-establish subsequent to burning.

2. STUDY AREA

2.1 Elk Island National Park

2.1.1 Location

Elk Island National Park is located approximately 37 km east of Edmonton, Alberta, and comprises an area of 19,680 ha (Figure 1). The park is situated in a region of morainal deposits known as the Cooking Lake Moraine, and is elevated some 30-60 meters above the surrounding lacustrine plain (Crown 1977). This slight increase in elevation causes the park to receive somewhat more precipitation than the surrounding area. Consequently, boreal forest vegetation occurs here as an isolated pocket surrounded by aspen parkland (Rowe 1972).

2.1.2 Climate

Elk Island National Park lies within the humid continental climate region, and experiences warm summers and cold winters. January and July temperatures average -14.5°C and +16.5°C, respectively, but may range from -40°C to +32°C. The average annual precipitation is 43 cm, 70% of which falls as rain during the growing season. Annual snowfall is about 130 cm, and generally remains from December to April. The growing season lasts about 175 days,

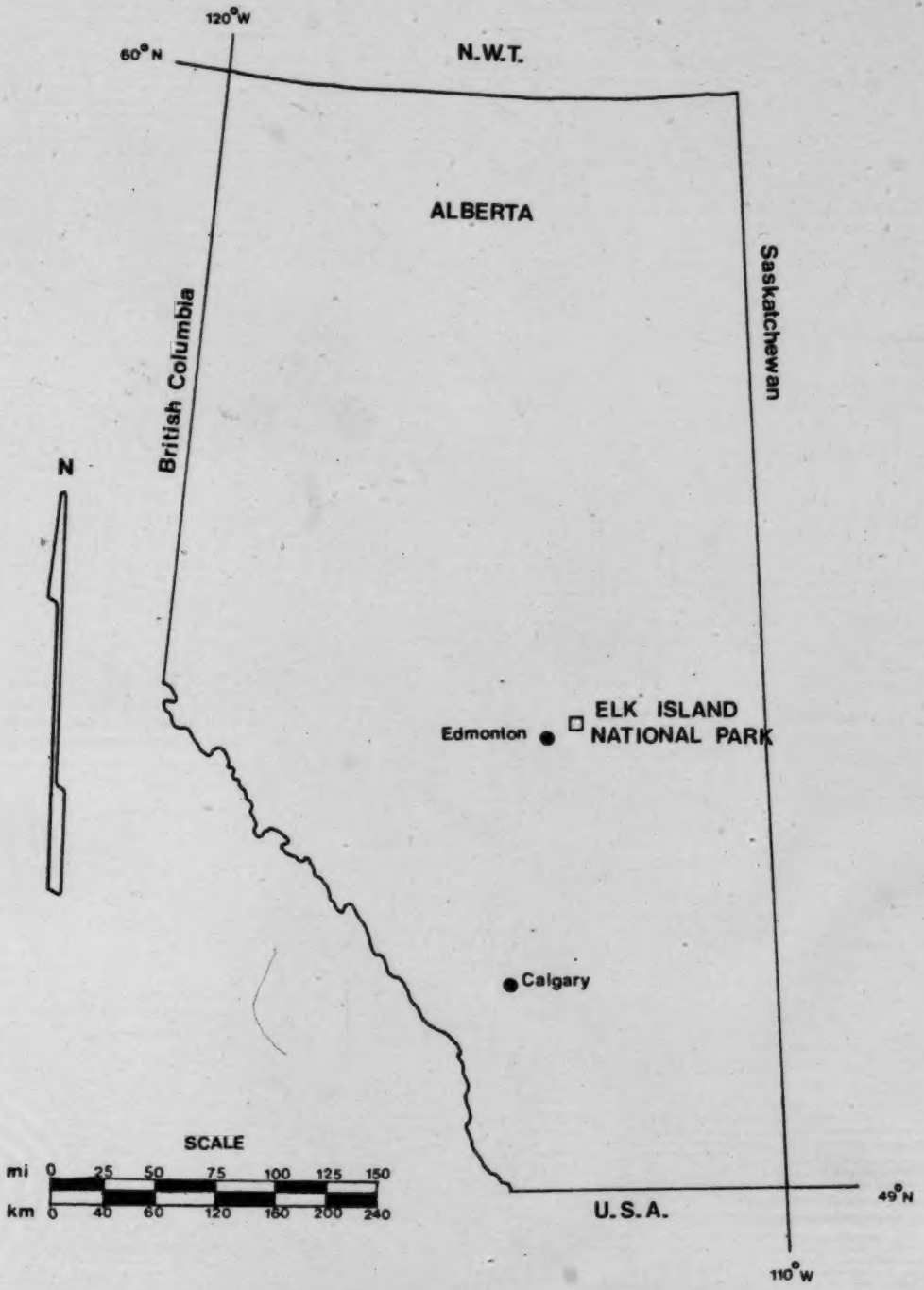

Figure 1. Location of Elk Island National Park, Alberta.

from the beginning of May to the middle of September (Scace 1976).

2.1.3 Vegetation

Elk Island National Park is classified as an outlying portion of the Mixedwood Section of the Boreal Forest Region (Rowe 1972). Polster and Watson (1979) recently completed a detailed description and analysis of the vegetation within the park. In general, the overstory vegetation consists of trembling aspen (Populus tremuloides) and balsam poplar (Populus balsamifera), while prickly rose (Rosa acicularis), wild red raspberry (Rubus strigosus), and beaked hazelnut (Corylus cornuta) are common in the understory. These species occur on mesic upland sites that have been disturbed by fire within the last 100 years (Polster and Watson 1979). White spruce (Picea glauca) may be present in the overstory of undisturbed stands. Open grassy sites are dominated by Agropyron subsecundum and Calamagrostis canadensis. Vegetation on wet "bog" sites consists of black spruce (Picea mariana) with Ledum groenlandicum, Vaccinium vitis-idaea, and Sphagnum spp. as important understory species.

2.1.4 Topography and Soils

Crown (1977) recently completed an excellent survey of the topography and soils of Elk Island National Park. The topography is characterized by numerous hills and

depressions, and the local relief rarely exceeds 15 meters, (Crown 1977). The most extensive soils are classified as Luvisols according to the Canadian System of Soil Classification, (C.S.S.C. 1978). Areas of grassy vegetation are found on soils of the Dark Gray Luvisol subgroup, while Orthic Gray Luvisols occur in forested areas (Crown 1977). Humic Luvic Gleysols, Rego Gleysols, and Gray Solidized Solonetz subgroups occur in areas of poor drainage or groundwater discharge (Crown 1977).

2.1.5 Animal Populations

Large herds of native ungulates are the main attraction of the park, as well as the primary management activity. Manitoba wapiti (Cervus canadensis manitobensis), Rocky Mountain mule deer (Odocoileus hemionus hemionus), white-tailed deer (Odocoileus virginianus dacotensis), northwestern moose (Alces alces andersoni), plains bison (Bison bison bison) and a rare herd of woods bison (Bison bison athabascae) all occur in large numbers. Moose are particularly important to this study because of their heavy browsing on hazel shrubs. Approximately 500 head of moose and 600 head of plains bison occur in the area of the park included in this study (Parks Canada 1976). The animals are confined to the park by a 2.5 meter high fence. The resulting grazing pressure has had a substantial impact on the vegetation in the park, reducing the stature of the shrub layer and in some areas reducing the amount of aspen

regeneration (Polster and Watson 1979).

2.1.6 Fire History

Kjorlien (1977) reviewed the history of fire occurrence in Elk Island National Park. This region was subjected to periodic fires from both natural and man-caused ignition. Prairie grass fires were common following dry lightning storms (Nelson and England 1971), and natives frequently burned off grassy areas to increase forage for horses (Thomas 1977). Prior to settlement, fires which initiated in the grasslands to the east were capable of spreading into the park when accompanied by strong winds and large areas of continuous fuels.

The advent of settlement in the late 1800's increased the incidence of fires. Increased agricultural development and the presence of large settlements soon led to the establishment of a fire prevention program (Kjorlien 1977). The last major fire to sweep through the area was in 1895, and burned virtually the entire park. This fire was due to a combination of extremely dry spring weather and a large number of land-clearing fires set by the local inhabitants. It was reported that the fire was so intense that hardly a tree was left standing and that all of the animals in the park were destroyed (Kjorlien 1977). Other small fires occurred in the park in 1937 (about 500 ha) and 1946 (450 ha). Neither of these fires burned in the present study area.

The lack of large fires in the park in recent times is due to a combination of factors. First, suppression equipment and methods have improved substantially, allowing rapid control of fires while they are still small. Second, the fuel complex has changed, both within and outside of the park. Historically, fires began in the large, continuous grasslands to the east (Nelson and England 1971). These fires often swept across the prairies and into the park. Presently, the large amount of cultivated land surrounding the park acts as a fuelbreak which prevents fires from spreading. In addition, fuels inside the park have changed as well. Prior to the large fire of 1895, coniferous vegetation was much more prevalent than it is today (Kjorlien 1977). The large fire of 1895 eliminated much of the spruce and pine from the park, reducing the amount of highly flammable coniferous fuels. Grazing by wild ungulates has also reduced the total fuel build-up in the park.

2.2 Study Site

2.2.1 Location

The study site is located in the central portion of Elk Island National Park, in the middle of Sec.22, T53, R20, west of the fourth meridian (Figure 2). The site lies about 0.75 km east-southeast of Tawayik Lake, and comprises an area of about 4.2 ha. The site is flat, with a gentle wet

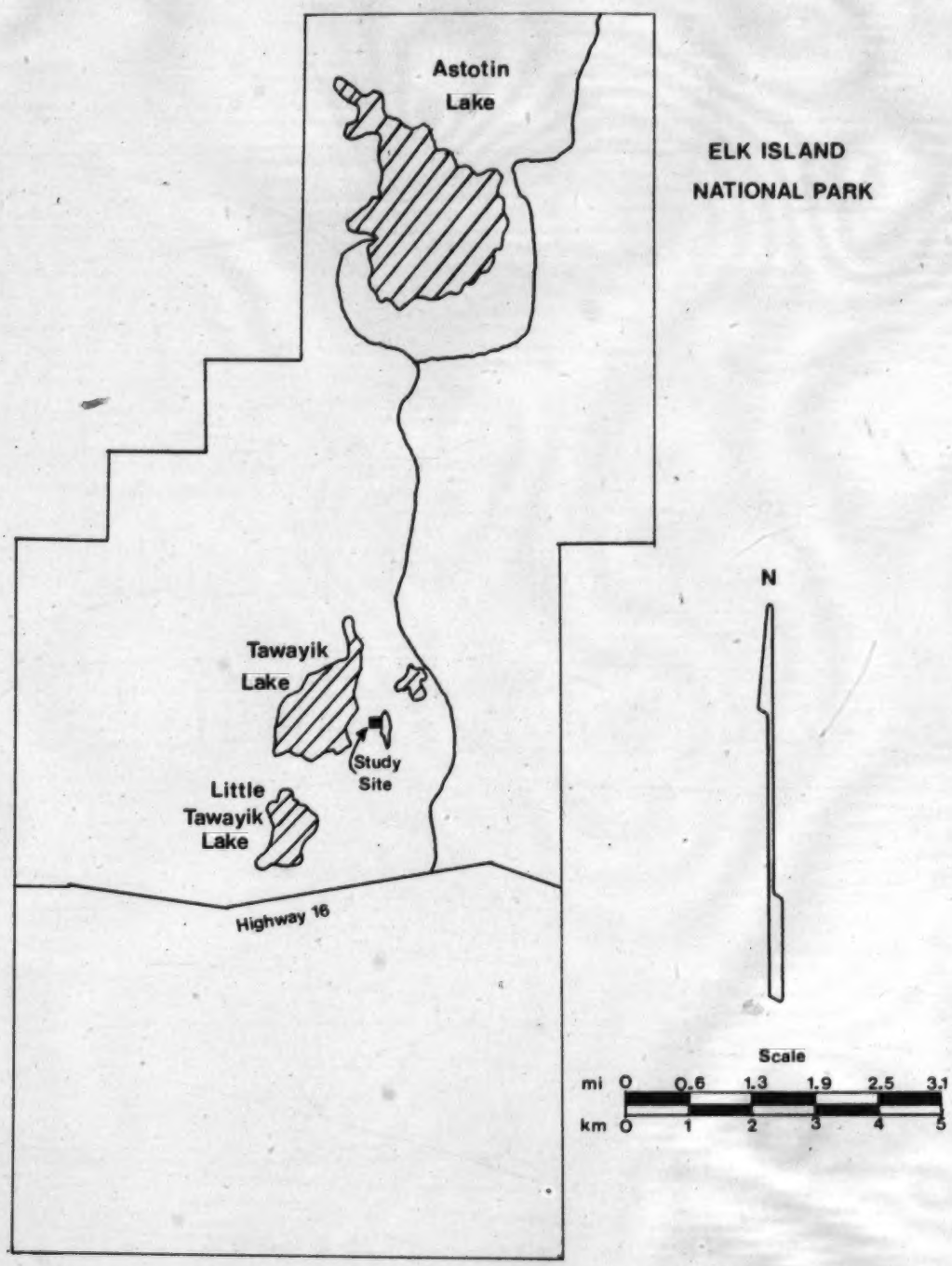

Figure 2. Location of study site within Elk Island National Park.

depression in the center. A steep bank descends about 2 meters to an unnamed lake on the eastern edge of the site.

2.2.2 Soils

The soils on the site were classified as Orthic Gray Luvisols, based on samples taken during this study. This is a well drained soil, originating from fine textured glacial till (Crown 1977). Fertility of these soils is good, with high levels of P and K, but levels of N are low (Crown 1977). The organic layer was composed of distinct L, F and H layers, and averaged 4.7 cm in depth.

2.2.3 Vegetation

The vegetation on the study site falls into the Taraxacum Sub-type of the Corylus-Rosa Upland Group as described by Polster and Watson (1979). The site is dominated by an overstory of trembling aspen and balsam poplar. Crown cover of these species ranged from 36 to 87%. Heavy aspen and balsam poplar reproduction was present in openings under the canopy. The overstory trees were cored with an increment borer in an attempt to determine the age of the stand, but heart-rot prevented an accurate age determination. The best estimates available using the increment cores indicated that the ages of the oldest trees ranged from 50 to 70 years. In addition, cross-sections were taken from hazel stems and age determinations made. Growth rings on 15 hazel cross-sections were counted, and the

average age of the stems was 6.9 years.

The shrub stratum on the site consisted mostly of beaked hazelnut and wild red raspberry. Other common shrubs included wild gooseberry (Ribes hirtellum), prickly rose (Rosa acicularis), Saskatoon-berry (Amelanchier alnifolia), Canadian buffalo-berry (Shepherdia canadensis), and snowberry (Symphoricarpos albus).

Herbs present included Erigeron acris, Lathyrus ochroleucus, Vicia americana, Taraxacum officinale, Plantago major, Fragaria virginiana, and species of Calamagrostis and Agropyron.

2.2.4 Fuel Complex

The fuel complex on the study site consisted of aspen and balsam poplar leaf litter under the tree canopy and grass in the open spots. Dead and down woody fuel contributed very little to the total fuel complex, although there were some downed aspen stems scattered throughout the study site. The shrub stratum also contributed to the fuel complex. Wild gooseberry in particular added significant amounts of fuel in isolated spots. In the wet areas along the lake shore, heavy stands of grass added significantly to the total fuel loading. Moose and buffalo trails up to 1 meter wide were common throughout the area. These gaps in the fuelbed often slowed or stopped the spread of the fire. Dried buffalo droppings also contributed to the fuel complex, and may be important as sites for holdover fires

(Wright and Bailey 1980).

3. LITERATURE REVIEW

3.1 General

The role of fire as an agent of disturbance and renewal in the boreal forest has received intensive study, especially in the last decade (Kelsall et al. 1977). Fire is beginning to be accepted as an integral part of the boreal ecosystem, having been present for thousands of years and responsible to a large degree for the present character of the vegetation (VanWagner 1979). Many studies have established the historical presence of fire, and the general effects of periodic burning have been well documented (Wright and Heinselman 1973). Recently, several ecological reviews of fire in the boreal north have been published (Slaughter et al. 1971, Heinselman 1973, Viereck 1973, Rowe and Scotter 1973, Kelsall et al. 1977). The purpose of this chapter is not to review all of the literature available concerning fire and its effects on boreal ecology, but to concentrate on those studies dealing with the specific aspects of the effects of fire on plants.

3.2 Effects of Fire

Fire affects plant communities in three ways. First, fire consumes plant material. Vegetation is a source of fuel for the combustion process; specifically, the physical and chemical characteristics of the vegetation control the degree of fire disturbance. Second, heat from a fire kills or injures plants, depending on the fire disturbance level and characteristics of the plants being disturbed. Third, fire has direct and indirect effects on other biotic and abiotic components of an ecosystem, including animals, insects, diseases, water and microclimate.

3.2.1 Vegetation as Fuel

Fire is unique among natural disturbances in that the vegetation being disturbed controls the extent and severity of the disturbance (Woodard 1977). Other disturbances such as hurricanes, landslides or floods may be altered somewhat by the vegetation being disturbed, but a fire is dependent on the characteristics of the vegetation as fuel for its ignition and propagation.

Fire disturbance level is determined by several physical and chemical characteristics of vegetation. Chemical characteristics determine flammability, and include the heat of combustion of a fuel particle (Brown and Davis 1973), the mineral content of the vegetation (Philpot 1968), the amount of volatile compounds present (fats, oils, resins, etc.) (Albini 1980), and the moisture content of the

fuel particle (Schroeder and Buck 1970). Physical characteristics of fuel and fuelbeds also have a large impact on fire disturbance level. Particularly important is the physical arrangement of the fuel particles. Continuity in the horizontal plane influences the forward rate of spread of a fire (Brown and Davis 1973), and vertical continuity determines the potential for crown fires (VanWagner 1977). Physical arrangement of fuel particles also influences rate of moisture loss and availability of oxygen within the fuelbed (Rothermel 1972). Important measures of fuel arrangement include packing ratio and surface area to volume ratio. The packing ratio is a measure of the fraction of the fuelbed volume that is occupied by the fuel particles, and provides an estimate of the compactness of the fuelbed (Rothermel 1972). Surface area and volume are important in determining heat transfer and moisture relationships within individual fuel particles. The ratio of surface area to volume combines the two quantities and can be used to indicate the size of the fuel particle (Brown 1970).

3.2.2 Plant Mortality

Fire has a direct impact on vegetation by killing or injuring plant tissue. Combustion produces gas temperatures high enough to damage living cells (Hare 1961). Forest fuels begin to burn at about 380°C, and peak flame temperatures often exceed 1000°C. (Brown and Davis 1973). Many studies

have attempted to determine the temperatures lethal to plant tissue, but differences in study design and measurement methods make it difficult to compare these results (Wright 1970). Brown and Davis (1973) suggest a temperature of 140°F (60°C) as "a useful level to keep in mind". Kayll (1963) found temperatures of 60°C for 2-4 minutes and 65°C for less than two minutes to be lethal to Scots pine (Pinus sylvestris L.) seedlings. Wright (1970) subjected two species of bunchgrass to various combinations of time and temperature. He found death occurring when plants were subjected to temperatures as low as 48.9°C for 130 minutes and as high as 93.3°C for 0.5 minutes. These studies seem to indicate that plant mortality is a function of two variables: sufficiently high temperature and length of exposure.

Several factors determine a plant's susceptibility to heat damage. Brown and Davis (1973) present a list of nine factors controlling heat injury to trees. They include: 1) initial temperature of vegetation, 2) size and morphology of critical tree portion exposed to injury, 3) thickness and insulating properties of bark, 4) branching and growth habit, 5) rooting habit, 6) depth of organic matter covering mineral soil, 7) flammability of foliage, 8) stand habit, 9) season and growth cycle. Various portions of a plant may vary in susceptibility to heat injury. Stems of plants, especially trees, are often well protected by thick bark and usually show the least damage from a fire (Brown and Davis

1973). Roots, because of their thin epidermal covering, are more prone to damage (Kayll 1968). Roots within the mineral soil zone may be well protected, but those that lie in or near the organic layer are easily damaged if organic matter is consumed by a fire (McLean 1969). Foliage is perhaps the most vulnerable to heat injury (VanWagner 1973). Foliage is unprotected by insulating material, and often contains highly flammable oils and resins (Brown and Davis 1973). Needles and leaves are usually small enough that internal temperatures are quickly raised to lethal levels (Brown and Davis 1973). Some researchers have suggested that foliage damage is more important than cambial damage in causing tree mortality (VanWagner 1973).

3.2.3 Fire and Reproductive Mechanisms

Fire also has an impact on the reproductive mechanisms utilized by plants. Many different types of regenerative mechanisms are utilized in post-fire plant re-establishment, and plants may respond quite differently to burning depending on the regenerative mechanisms utilized. Kellman (1970a) lists three factors important in determining the nature of post-fire succession: 1) residual flora not destroyed by the fire, 2) regrowth from buried, viable propagules, 3) species present that can quickly reach the site due to efficient dispersal mechanisms. Noble and Slatyer (1977, 1980) have divided the methods of post-fire re-establishment into four categories: 1) those that utilize

seed arriving from outside the disturbed area, 2) those that utilize seed buried in the soil, 3) those that utilize seed stored in the canopy, 4) those that resprout from underground organs. Rowe (1979), in adapting this scheme to boreal plant species, adds a fifth category: those that persist by being resistant to damage by fire and continue to grow subsequent to burning.

3.2.3.1 Disseminated Seed

Plants reproducing from seed disseminated by off-site individuals will be affected by fire disturbance level and size of fire. Connell and Slatyer (1977), in their paper outlining the mechanisms of succession, include intensity and area of disturbance as the major factors determining the outcome of secondary succession. Fire disturbance level determines the number of individuals killed or injured, which regulates the number of seed sources available for re-establishment on the burn area (Connell and Slatyer 1977). Fire disturbance also determines the characteristics of the seedbed available to migrating seed (Shearer 1975). Severe fires may create large quantities of ash, which may be toxic to young seedlings (Ahlgren 1959). Low severity fires may not remove sufficient organic matter to allow the radicle to penetrate to mineral soil (Chrosciewicz 1976). Easily disseminated seed is usually quite small and contains low levels of carbohydrate reserves (Archibold 1980). Extensive fires may create areas too large for even small,

wind disemminated seed to repopulate (Connell and Slatyer 1977).

3.2.3.2 Buried Seed

Plants may reproduce subsequent to disturbance through the germination of seed buried in the soil. There is a large body of literature pertaining to the role of buried seed in old-field succession (Oosting and Humphreys 1940, Egler 1954, Major and Pyott 1966, Livingston and Allessio 1968). All of these studies suggest that buried seed is important in determining the species composition of the initial plant community following disturbance.

Several studies have recently examined the role of buried seed in forest regeneration as well. Marquis (1975) extracted duff cores from a northern hardwood stand in Pennsylvania. He found that seed densities of up to 2.5 million per hectare were common, and observed three types of germination behavior. Sugar maple (Acer saccharum Marsh.), eastern hemlock (Tsuga canadensis (L.) Carr.) and American beech (Fagus grandifolia Ehrh.) all germinated the year after seed release. Black cherry (Prunus serotina Ehrh.), white ash (Fraxinus americana L.), yellow poplar (Liriodendron tulipifera L.), red maple (Acer rubrum L.) and yellow birch (Betula alleghaniensis Britton) all germinated over a period of several years following dispersal. Pin cherry (Prunus pennsylvanica) seed was stored in the soil for long periods, and quantities of viable seed could be

found up to 30 years following dissemination. Marks (1974) has also documented the role that buried pin cherry seed plays in vegetation recovery following disturbance in northern hardwood stands.

Kellman (1970b) sampled the duff and upper soil layers in a coastal douglas-fir (Pseudotsuga menzesii) forest in British Columbia. He found nearly 70% of the seed buried in the soil to be from red alder (Alnus rubra Bong.). He suggested that the seed stored in the forest floor may have been deposited following the last fire (nearly a century previous) or after recent logging activity. It was also suggested that buried seed plays an important role in secondary succession on these sites.

Post-fire plant communities in the northern Rocky Mountains of Montana have also been shown to be heavily dependent on buried seed (as well as resprouting) for initial re-establishment following fires of low to moderate severity (Lyon and Stickney 1976). Thirty-three percent of all regeneration on these burns originated from buried seed. Stickney (pers. comm.)[1] suggests that the initial species composition of these communities is derived almost exclusively from plants regenerating from on-site propagules.

Ahlgren (1960) found that 30% of the post-fire regeneration in northern Minnesota was from buried seed. In

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[1] Peter Stickney. Associate Plant Ecologist, U.S. Forest Service, Missoula, Montana. Personal communication, 1981.

later studies, he found that quantities of seed stored in the soil vary according to time since disturbance (Ahlgren 1979a) and type of disturbance (Ahlgren 1979b). He also found that soil cores from a stand burned by wildfire produced many more seedlings under greenhouse conditions than did unburned soil cores (Ahlgren 1979c).

Archibold (1979) removed soil samples from a post-fire site in northern Saskatchewan. He found that 87% of the resulting seedlings came from buried seed, and that about half of these were tree species (Betula papyrifera, Populus tremuloides and Picea glauca). He also suggests that revegetation of the area should proceed rapidly due to the large amount of seed present on-site.

Moore and Wein (1977) studied seedling emergence from soil cores taken from various forested sites in New Brunswick. The number of viable seeds decreased along a gradient from deciduous dominated stands to coniferous stands to organic soil/bog sites. The majority of seed was stored in the upper organic layers of the soil within 2 cm of the surface. Wild red raspberry (Rubus strigosus) accounted for over 90% of the seedlings. Ungerminated seed in the soil was predominantly Betula spp. They suggested that fire intensity is an important factor in determining the species composition of the post-fire plant community. Since most of the seed was stored in the upper organic layers, a fire which removed a portion of the organic layer would also remove a large amount of potential regeneration

(Moore and Wein 1977).

3.2.3.3 Canopy-stored Seed

Another reproductive strategy utilized by plants in post-fire re-establishment is the storage of seed in the canopy (Noble and Slatyer 1977). This strategy is utilized by some forest trees in North America and by some species of shrubs in Australia. Common examples of this habit in the boreal forest include lodgepole pine (Pinus contorta var. latifolia), jackpine (Pinus banksiana) and to some extent black spruce (Picea mariana) (Fowells 1965). The first two of these species possess cones whose scales are bonded together by resin. It is generally assumed that the high temperatures that accompany forest fires melt the resin bonds, allowing the cones to open and release their seed (Lotan 1976). However, recent evidence indicates that moisture content of the cones and other environmental factors have a large impact on seed release (Hellum and Pelchat 1979, Hellum and Barker 1980). Several species of shrubs in Australia also utilize this strategy, including members of the genera Banksia, Casuarina, Hakea, Leptosperma, and Petrophila (Beadle 1940, Gill 1977). Fire disturbance level may have a large impact on the ability of these species to re-establish themselves. A low intensity fire may provide insufficient heat to melt the resin bonds, or a fire of very high intensity may actually consume the cones or decrease seed viability. In addition, fire may not

prepare an adequate seedbed, depending on the amount of organic matter removed.

3.2.3.4 Resprouting

The fourth strategy used by plants in post-fire re-establishment is resprouting from subterranean organs (Noble and Slatyer 1977). This group comprises a wide variety of species, and seems to be especially common in ecosystems subject to frequent disturbance by fire (Lyon and Stickney 1976, Rowe 1979). Resprouting can be a very advantageous method of regeneration. These plants can resprout immediately following disturbance, taking advantage of the increased levels of nutrients, light and water that become available (Flinn and Wein 1977). They are also immediately present on site following disturbance, and need not expend precious resources becoming established (Lyon and Stickney 1976). Fire disturbance level directly affects reproduction from underground organs (Flinn and Wein 1977). The most important factor controlling the effect of fire on subterranean parts is depth of duff and soil covering them. McLean (1969) has classified the common ground cover species in the Douglas-fir Zone of British Columbia by their resistance to damage by fire. He rates their resistance according to their depth of rooting and root morphology. His categories are:

1. Susceptible - those that have fibrous root systems or rhizomes above the mineral soil;

2. Moderately resistant - those with fibrous root systems or rhizomes less than 5 cm. below the mineral soil surface; and
3. Resistant - those with rhizomes growing between 5 and 13 cm below the mineral soil surface horizon.

Flinn and Wein (1977) measured the depths at which underground organs of various species of understory plants occur in New Brunswick. The species they observed had reproductive organs in three different layers of the forest floor: The litter layer, the F-H layer, and mineral soil. They suggest that the most important variable determining the outcome of disturbance by fire is fire intensity, and that post-fire plant succession could be predicted using knowledge of rooting depth and fire intensity. In addition, they suggest that plants with reproductive organs occurring deep in the mineral soil will be able to survive a more intense fire than will seed stored in the litter layer, and hence will more likely be present in the post-fire plant community.

Lyon and Stickney (1976) found that from 40 to 75% of all post-fire reproduction resulted from resprouting in the northern Rocky Mountains. Ahlgren (1960) found that 2/3 of all reproduction following fire in northern Minnesota was from resprouting, and Buckman (1964) found vigorous resprouting in beaked hazelnut (Corylus cornuta) in the same area. Lutz (1956) observed that resprouting was a very important mechanism for regeneration following fire in

Alaska. Wright (1972), in his review of shrub response to fire, reports that resprouting is important in reproduction in nearly all ecosystems where shrubs occur. Miller (1977) found that blue huckleberry (Vaccinium globulare Rydb.) resprouted profusely following spring burning in Montana, but was nearly eliminated by burning in the fall. Greater mortality following fall burning was due to lower duff moisture contents and large amounts of sufficiently dry large diameter fuels.

3.2.4 Indirect Effects

Fire also has indirect effects through impacts on other components of the ecosystem. These effects include changes in microclimatic conditions due to vegetation removal, changes in other biotic factors, and changes in soil characteristics. All of these changes have important implications for the re-establishment of vegetation following fire.

Changes in post-fire environment have not been well documented. Most research has concentrated on post-fire plant community composition, and little emphasis has been placed on changes in the abiotic environment and its effect on plant establishment. Changes that have been documented include increases in soil surface temperature due to the blackened surface (Helvey et al. 1976, Fowler and Helvey 1978), and increased exposure to wind (Brown and Davis 1973). Woodard (1977) discusses the influence of residual

fuel particles left after burning on subsequent plant re-establishment. He found that large residual fuel particles often act as "safety areas" which may protect seeds or young plants from heat injury. Soil moisture availability also varies considerably following fire. Soil moisture may increase due to removal of vegetation and reduced transpiration (Helvey et al. 1976) or it may decrease due to reduced infiltration and increased erosion (Ahlgren and Ahlgren 1960, Wells et al. 1979).

Changes in the biotic environment following burning are somewhat better documented. The increased heat and light levels may either attract or repel birds and small mammals, and the succulent new growth is often preferred as forage by large ungulates (Lyon et al. 1978). Changes in ungulate foraging habits may in turn affect the re-establishment of vegetation on the burned site (Lyon et al. 1978). The effect of fire on insect populations is variable; they may increase or decrease depending on the severity of the fire and the season in which the fire occurs (Ahlgren and Ahlgren 1960). Plant diseases are often controlled by burning; a well known example is prescribed burning in the southeastern U.S. for control of brown needle spot disease (Scirrhia acicola (Dearn.) Sigg.) (Fowells 1965). Smoke from pine needle and grass fires has been shown to have adverse effects on various plant diseases (Parmeter and Uhrenholdt 1976). Competitive interactions between plants are also affected by burning. In less severe fires, certain plants may be killed

while others survive; this alters species interactions in competition for resources. More severe fires may remove all vegetation and generate large quantities of nutrients. Plants will be competing for these nutrients, and the most successful will become established at the expense of the others (Grime 1979, White 1979).

The effects of fire on soil is one of the better documented fields of fire research. Several reviews are available, of which two were consulted in this study. Ahlgren and Ahlgren (1960) include an excellent section on fire's effects on soil in their landmark paper "Ecological Effects of Forest Fires". More recently, The U.S.D.A. Forest Service National Fire Effects Workshop has published a complete review of recent literature relevant to North America (Wells et al. 1979). No attempt will be made here to review all of the effects of fire on soil, but to summarize those effects most important to plant re-establishment.

Fire, through the oxidation of plant biomass, makes available large quantities of nutrients necessary for plant growth. Most researchers have found increased levels of Ca, Mg, P and K ions in the upper soil layers (Wells et al. 1979). Soil pH is usually increased due to the influx of large amounts of basic cations (Wells et al. 1979). Organic matter is often decreased as the result of burning, which may reduce the cation exchange capacity and nitrogen availability of the soil (Ahlgren and Ahlgren 1960). Nitrogen is usually reported to decrease due to

volatilization following burning, but may be rapidly replaced through ammonification, increased microbial activity and the establishment of nitrogen fixing vegetation (Raison 1979). Fire has an impact on the physical properties of soil as well. Water-repellant layers may be formed some distance below the soil surface (DeBano et al. 1977), and reductions in bound water may occur (Kohnke 1968). Finally, fire affects the biology of the soil. Intense heating can sterilize the soil by killing soil micro-organisms and meso-fauna. This may reduce nitrification, litter decomposition and soil aeration (Ahlgren,I. 1974, Wells et al. 1979).

3.3 Models of Fire Effects

As the previous review indicates, the effects of fire are a complex set of interactions between the biotic and abiotic components of an ecosystem. The outcome of a fire in a plant community is therefore very difficult to predict. However, several workers have recently attempted to develop models that summarize the characteristics of fire-prone vegetation, and in some cases, predict the outcome of disturbance by fire.

The most well-known of these is the "vital attributes" model of Noble and Slatyer (1977, 1980). Their model is based on the mechanisms of succession as outlined by Connell and Slatyer (1977), and includes those plant characteristics

that determine the response of a plant community to fire. Noble and Slatyer (1977) list 4 such characteristics:

1. Method of arrival or persistance of propagules;
2. Conditions under which the species establish and grow to maturity;
3. The longevity of individuals, and the time taken to reach critical stages in their life history; and
4. Growth rate of the species.

They have tabulated these attributes for species occurring in southwest Australia, and use them to predict the impact of fire on the plant communities where these species occur. Cattelino et al. (1979) have applied this model to several plant communities in the northern Rocky Mountains, and use it to predict the outcome of fire disturbance. This model has been further developed by Kessel and Potter (1980) to include specific predictions of the effects of fire disturbance. Tree reproduction, understory species and the effects of different scorch heights are all quantitatively predicted. Rowe (1979) has adapted the vital attributes model to plant species in the boreal forest, but cautions that prediction of ecosystem succession must also take into account allogenic factors which have an impact on the post-fire plant community.

Davis et al. (1980) have developed a model describing the fire ecology of ten "fire groups" in northwestern Montana. This model is based on the habitat types of Pfister et al. (1977) and presents a "simplified, synthetic overview

of fire's role in succession for all habitats of each fire group" (Davis et al. 1980). Each "fire group" is accompanied by a flow diagram showing the successional pathway it follows subsequent to disturbance by fire.

Polster and Watson (1979) have developed a diagram outlining the pattern of post-fire succession on mesic forest sites in Elk Island National Park, Alberta (Fig. 3). Their model takes into account fire severity and the species composition of the burned stand. However, they admit that fire has effects other than the ones shown, and that other factors such as grazing have also had an effect on successional development. In addition, their model fails to quantify fire disturbance level, and does not recognize the fact that fire also may occur in other plant communities in the park.

3.4 Fire Disturbance Level

It is apparent from the foregoing review that fire disturbance level is an extremely important variable in determining the effects of fire on plants. Woodard (1977) reviewed the role of fire disturbance measurement in fire research and concluded that most researchers are aware of its importance. However, fire disturbance level is seldom documented at the time of burning (Woodard 1977). It is difficult to measure during an ongoing fire due to the harsh conditions present, and areas burned by wildfire can only be

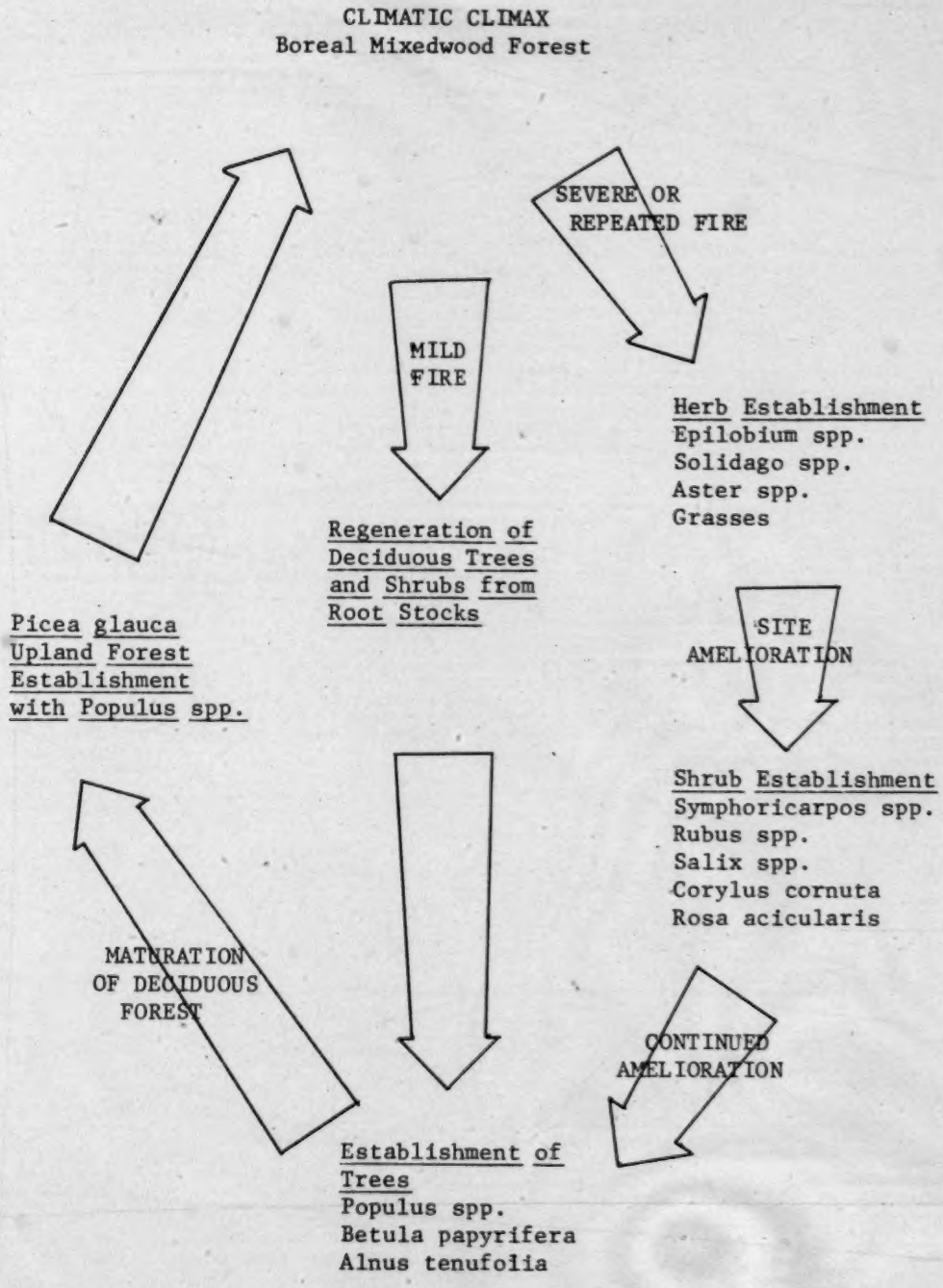

Figure 3. Successional pathways followed by upland vegetation following fire in Elk Island National Park. (After Polster and Watson 1979).

investigated after the fact. In addition, much confusion exists among researchers concerning the measures of fire disturbance level (Woodard 1977, VanWagner and Methven 1978). Because of the importance of this variable and the confusion surrounding its measurement, the following section will briefly discuss the various methods of documenting fire disturbance level.

3.4.1 Temperature

The most common method of documenting the thermal environment of a fire is by measuring the temperatures reached during burning. Many methods of temperature measurement have been used. Early researchers used bulb thermometers placed in the soil to measure heat penetration (Beadle 1940). They are inexpensive and easy to use, but are often slow to respond to temperature changes and do not record exposure times. Chemicals with known melting points are becoming more popular, especially in measuring soil and ground surface temperatures (Beadle 1940, Whittaker 1961, Kilgore 1972, Shearer 1975, Bailey and Anderson 1980). Although they are easy to use, their drawbacks include 1) the chemicals are greatly affected by gas velocities, 2) the temperatures recorded are maximum, and 3) they do not record exposure times (Woodard 1977). Thermocouples are perhaps the most accurate method for documenting temperatures. They have been widely used in all phases of fire research, including soil temperature measurement (Shearer 1975), temperatures

within live vegetative tissue (Wright 1970), and gas temperatures over flames (Walker and Stocks 1968). They enable the accurate measurement of temperature, and more importantly, enable the documentation of exposure times. However, their accuracy is often off-set by their bulk, complexity and expense (Whittaker 1961). Results may be affected by the sensing material used, the gas velocities experienced, and the location of the sensing junction (Walker and Stocks 1968, Woodard 1977). In addition, thermocouples require long wires to connect them to recording devices. In an intense fire, these connections may be destroyed or measurements may be distorted due to heating of the wires (Woodard 1977).

3.4.2 Fire Intensity

Fire intensity is another important measure of the thermal environment during burning. The term suffers from misuse, having been used to refer to air temperature, duration of heating, soil temperature, degree of stand destruction, and amount of forest floor consumed (Albini 1976). Technically, fire intensity refers to the rate of combustion of a fire. It can be expressed as rate of energy output per unit length of fire front (I_B) (Byram 1959), or as rate of energy output per unit area (I_R) (Rothermel 1972). In equation form, Byram's intensity can be written as:

$$I_B = H * w * r, \qquad (1)$$

where I_B = fireline intensity, in Kilowatts/meter;
H = heat of combustion, in kilojoules/kilogram;
w = weight of fuel consumed, in kilograms/meter^2,
r = rate of spread, in meters/second.

The second quantity, reaction intensity, is expressed as:

$$I_R = -\frac{dw}{dt} * H, \qquad (2)$$

where I_R = reaction intensity, in kW/m^2
$-\frac{dw}{dt}$ = mass loss rate/unit area, in kg/m^2-sec,
H = heat of combustion, in kJ/kg.

The major difference between the two measurements is that I_B expresses rate of energy output along a given length of fire front, while I_R expresses energy output rate over a given unit area. I_B is often used in fire control work as a measure of how close personnel can work to the fire line, or as an indicator of potential spotting (Albini 1976). I_R is an integral part of Rothermel's fire model (Rothermel 1972). This is a computer-based predictive model that determines rate of spread of a fire for a series of specified fuel types.

Reaction intensity (Rothermel 1972) and fireline intensity (Byram 1959) measure the rate of energy release, most of which is directed upward in the convection column (Byram 1959). In addition, fireline intensity in particular depends heavily on rate of spread, which is determined primarily by the presence of fine fuels (<7.6 cm in diameter) (Brown and Davis 1973). However, fine fuels do not

produce long residence times, which is very important in determining heat penetration into the duff layer (VanWagner 1972). Therefore, these measures may be appropriate for determining the potential for crown fires (VanWagner 1977) or spotting behavior (Albini 1979) but do not allow the accurate determination of heat flux to the duff layer. It is the duff layer which protects underground reproductive organs and buried seed (Flinn and Wein 1977, Moore and Wein 1977), and heat penetration into the duff may destroy most on-site germ plasm. VanWagner (1972) developed a model predicting duff consumption based on duff moisture, but it was derived entirely from empirical data, and may not apply to types of duff different from those upon which his study was based.

Other researchers have also recognized the drawbacks of fire intensity measurements when used to describe the impact of fire on vegetation. Viereck and Schandelmeier (1980) discuss this problem at length, and have proposed five fire severity classes based on the amount of duff and vegetation consumed by the fire. Similarly, Wells et al. (1979) developed three fire severity classes based on the percentage of the burned area that experiences light, moderate and heavy burning. Although these approaches focus on the impact of the fire on the organic soil layers, they depend on subjectively determined damage classes, and do not quantitatively describe the fire disturbance level occurring on the burn site or provide a basis on which to make

predictions. The approach taken by VanWagner (1972) and Albini (1975), that of attempting to quantitatively determine heat transfer and energy release resulting from duff combustion is probably the best, but will require much additional research in order to become of practical value.

Other methods have also been devised to estimate fire intensity. VanWagner (1973) developed a relationship that relates height of crown scorch in trees to fireline intensity. This relationship is mathematically expressed as:

$$h_S = 0.1483\ I_B^{0.667} \qquad (3)$$

where h_S = height of crown scorch, in meters;
I_B = fireline intensity, in kW/m

If equation (3) is solved for I_B, the following relationship is obtained:

$$I_B = 17.51\ h_S^{1.5} \qquad (4)$$

Equation (4) can be used to estimate the intensity of a fire by measuring the height of crown scorch. This relationship is based on empirical studies done in eastern Canada in red pine (Pinus resinosa Ait.) stands. Its application to the study of fire intensity in other stand types is currently unknown.

3.4.3 Total Heat Release

Another quantity used in estimating fire disturbance level is total heat release (Brown and Davis 1973, Albini 1976, Rothermel and Deeming 1980). It can be expressed as:

$$T = H * w, \qquad (5)$$

where T = total heat release, in kJ/m^2;
H = heat of combustion, in kJ/kg;
w = weight of fuel consumed, in kg/m^2.

Total heat release may be a more appropriate measure of fire disturbance level because it integrates energy output over the entire period of burning (Woodard 1977). It can be estimated using the heat of combustion and weight of fuel consumed as shown in equation (5), or it can be measured using various heat sensors: the passive recording heat flux indicator (Smith and Kelly 1971), the water-can analog (Beaufait 1966, George 1969), laminated tempered hardboard (Beaufait and Steele 1963), 18-kt gold sphere (Stockstad 1973) and the nitinol heat flux indicator (Smith 1973). All of these instruments have been calibrated in laboratory settings, but their application in the field has presented difficulties. Many of the instruments affect their own thermal environments through re-radiation of heat.

3.5 Artificial Fuelbeds

I am aware of only two previous studies that utilized artificial fuelbeds to generate controlled levels of fire disturbance in a field setting. Wright and Klemmedson (1965) studied the response of four species of bunchgrass to burning in southern Idaho. They packed shredded newspaper around each target plant and then placed a 55 gallon drum around each fuelbed to confine the fire. Fuel loadings were

determined previously by burning specified amounts of fuel and recording the resulting temperatures with Tempil. temperature pellets. The investigators chose to subject the plants to temperatures of 200°C and 400°C, so sufficient fuel was placed around the target plants to achieve the desired temperatures.

The major drawback to this approach is that factors other than fuel weight have a large influence on rate of energy output. Fuel arrangement is critical to heat output as it determines rates of combustion, oxygen availability, heat transfer, and moisture relations (Rothermel 1972). No attempt was made by Wright and Klemmedson (1965) to document or control fuel arrangement. In addition, duration of heating is a primary factor in determining plant mortality (Wright 1970), and was not recorded in the above study.

The second study utilizing artificial fuelbeds was performed by L.J. Lyon, wildlife biologist with the U.S. Forest Service in Missoula, Montana (Stickney pers. comm.).[2] In this study, Lyon packed varying amounts of aspen excelsior around selected wildlife forage plants and burned the fuelbeds. Results of the study were not published, and no further information was available concerning the methods used.

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[2]Peter F. Stickney. Associate Plant Ecologist, U.S. Forest Service, Missoula, Montana. Personal communication, 1981.

3.6 Fire Ecology of Hazel and Raspberry

The following section outlines the autecology of the two most important species considered in this study: beaked hazelnut (Corylus cornuta) and wild red raspberry (Rubus strigosus). Special emphasis will be placed on the mode of reproduction utilized by these species and their response to fire.

3.6.1 Beaked Hazelnut

Beaked hazelnut is a tall deciduous shrub that occurs throughout northern and eastern North America. Its range in Canada extends throughout the southern boreal forest from British Columbia to Newfoundland (Scoggan 1978). It is typically a resident of mesic forest sites and well drained soils (Maycock and Curtis 1960), and is usually associated with the Mixedwood section of the Boreal Forest Region in Alberta (Rowe 1972).

Hazel can reproduce by seed and resprouting from underground stems (Hsiung 1951). Good seed crops occur every 2-5 years, and the seed is usually disseminated by birds or small mammals (Schopmeyer 1974). Mature hazel stems begin producing seed at 2 years of age, and maximum seed production occurs at age 10 (Hsiung 1951). Reproduction of hazel by seed is usually limited to undisturbed sites. (Tappeiner 1971).

Hazel commonly reproduces from underground stems following disturbance (Hsiung 1951). Rapid resprouting

following fire has been reported by many authors. Ahlgren (1960) found hazel to resprout rapidly following fire in northern Minnesota and noted that it was still increasing in density five years after burning. He also reported that resprouting was more vigorous on drier burned sites than on wetter sites, and that soil drainage may be as important as fire disturbance level in determining the response of hazel to fire. Buckman (1964) observed that hazel resprouted profusely following spring burning, but found high mortality after burning in the summer. He attributed the summer mortality to decreased levels of duff moisture and consequent heat penetration. Number of sprouts on the spring-burned plots was still increasing four years following burning. Perala (1974) also found that resprouting of hazel was stimulated by prescribed spring burning in northern Minnesota. Ohmann and Grigal (1979) reported that basal area and density of hazel shrubs were still increasing five years following a spring wildfire in northeastern Minnesota.

Hsiung (1951) found that the underground stems of hazel usually occur at the interface between the duff and mineral soil layers. He found that 92.5% of all underground stems occurred within the top 15 cm of the soil. Buckman (1964) found duff moisture to be very important in determining the impact fire has on subsequent resprouting. Ahlgren (1960) reported that heating on moist soils is more damaging to underground stems than is heating on drier soils.

Hazel is commonly utilized as forage by moose and to some extent by deer (Hsiung 1951).

3.6.2 Wild Red Raspberry

Wild red raspberry (Rubus strigosus) is a low deciduous shrub occurring throughout northern and eastern North America. In Canada, its range extends from the southern border to the northern limit of the tree line (Hulten 1968). It is usually found on mesic upland forested sites and moist soils (Moss 1959).

Raspberry reproduces by sprouting and seed production, with each method utilized equally in recovery from disturbance (Ahlgren , C. 1974). Seed crops are produced annually, and are disseminated by mammals and birds (Schopmeyer 1974). Seed is also stored in the upper organic layers of the soil (Moore and Wein 1977).

Raspberry is commonly associated with recently disturbed sites, and is usually present in great numbers following disturbance. Populations subsequently decline, and within 5-10 years are often at very low levels (Ohmann and Grigal 1979). Foote (1976) included raspberry in her classification of post-fire successional communities in Alaska. She found raspberry present in the early successional communities, but reported that it disappeared within 5-10 years. Ahlgren (1960) found that raspberry was stimulated by burning, and Lutz (1956) reported that it resprouted vigorously after fire. Shafi and Yarranton (1973)

found raspberry to occur 1-5 years following fire in northern Ontario. Anderson and Bailey (1979) reported that raspberry was stimulated by annual burning over the short term (1-5 years), but Anderson and Bailey (1980) reported that raspberry populations decline when subjected to annual burning over longer periods of time (25 years). Some researchers have classified raspberry as a "fire follower" because of its preference for nitrogen-rich fire-disturbed soils (Hesselman 1917, Ahlgren, C. 1974).

Raspberry is not commonly utilized as forage in Elk Island National Park (Parks Canada 1976).

4. METHODS

4.1 General

This study had two relatively independent objectives. The first was to assess the effect of varying levels of fire disturbance on plant response; the second was to identify and quantify the regenerative mechanisms used in post-fire plant re-establishment. This section describes the methods used to achieve these objectives.

4.2 Fire Disturbance Level

A preliminary survey of the study site indicated that hazel was the most frequently occurring shrub on the burn area. Fifty fire disturbance plots were located throughout the study site, such that a hazel plant occupied the center of each plot (Fig. 4). Each target plant consisted of either a single aerial stem or a group of aerial stems associated with a single underground stem. Each plot measured 2 m x 2 m, and contained a smaller central plot 60 cm x 60 cm. The central plot delineated the limits of the artificial fuelbed. (Fig. 5).

Artificial fuelbeds were used to subject the target plants to controlled fire disturbance levels. All natural fuels were removed from the smaller central plot, and a 60 cm x 60 cm cardboard box with the bottom removed was placed

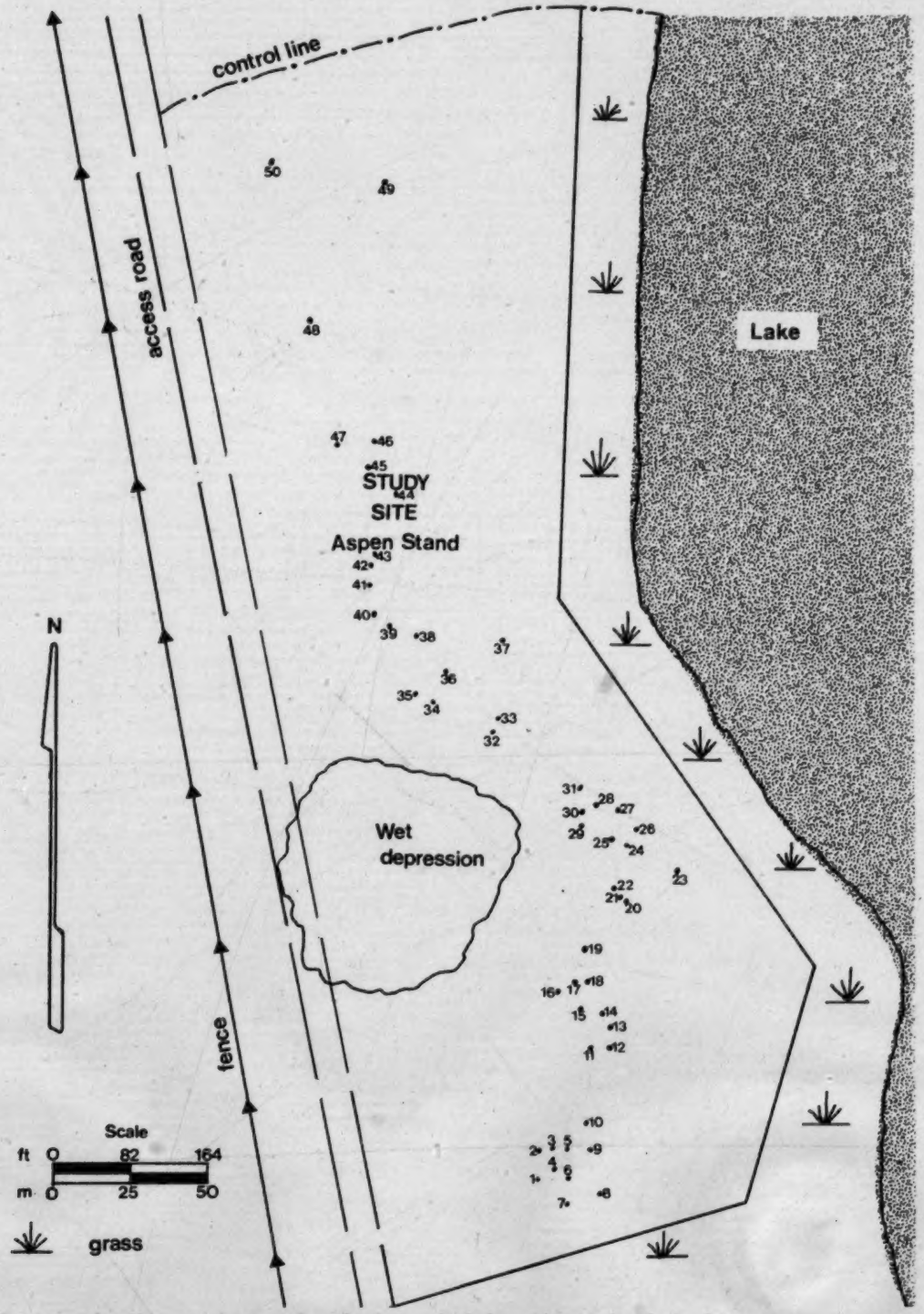

Figure 4. Location of plots within the study site.

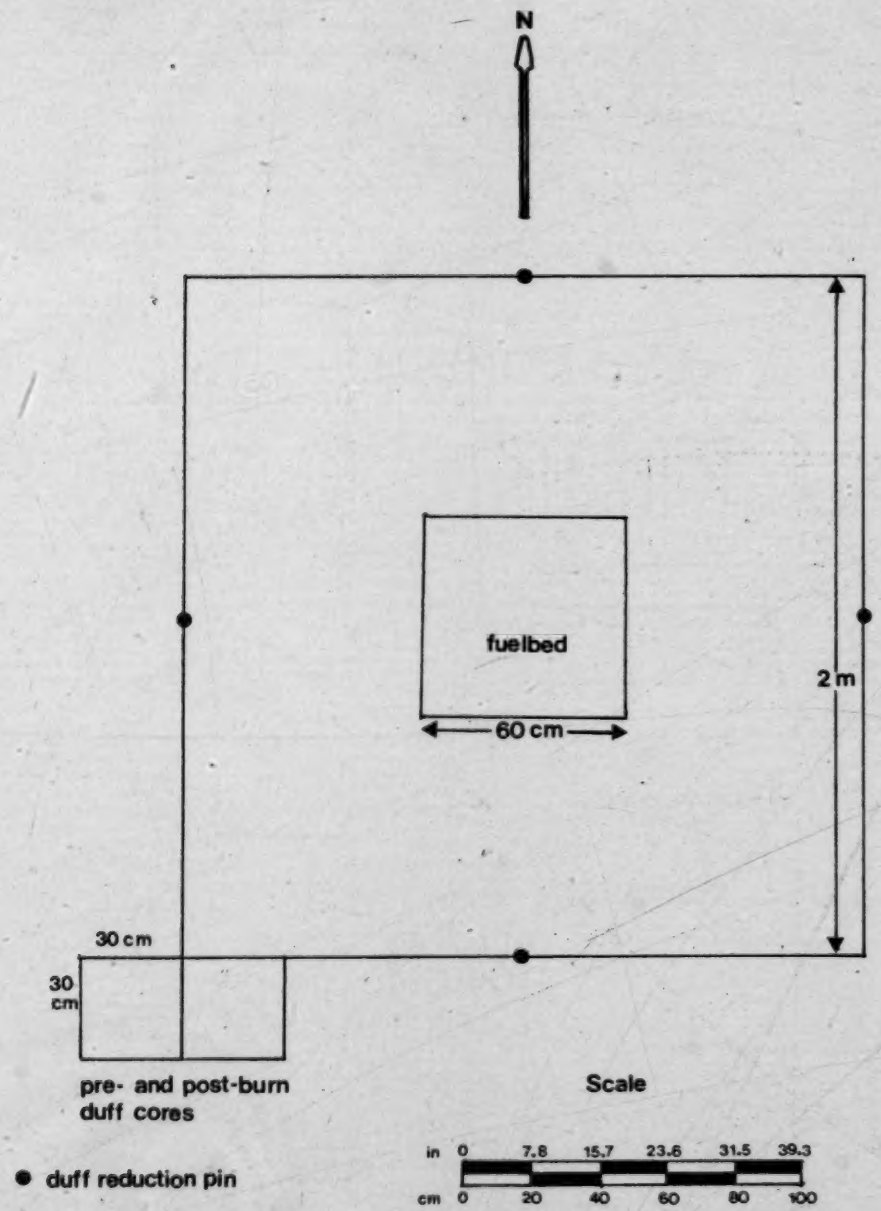

Figure 5. Diagrammatic representation of plot layout.

around each target plant. Excelsior packing material (shredded white spruce) was packed around the base of the plants inside the box. The height of each fuelbed was controlled, thus controlling the packing ratio in each fuelbed. The box was then removed, leaving the fuelbed in place around the target plants. Excelsior alone was not sufficient to achieve the highest fuel loading desired, so 24 45 cm x 2.5 cm x 2.5 cm white spruce slats were inserted into each of the heaviest fuelbeds as supplementary fuel.

Five levels of fuel loading were chosen, based on knowledge of existing fuel loadings and projected maximum loadings likely to be present in this fuel type (plates 1-5). Preliminary fuel measurements in Elk Island National Park by Dube (1979) indicated that natural fuel accumulations in aspen stands were approximately 0.87 kg/m^2. This value was chosen as an average fuel loading for the fuelbeds. In addition, lower fuel loadings were chosen to approximate light surface fuels (0.17 kg/m^2) and no fuel (0 kg/m^2). Heavier fuel loadings were chosen in an attempt to simulate the heaviest expected fuel accumulations (3.94 kg/m^2), and to cause maximum plant mortality (3.94 kg/m^2). These fuel loadings were based on aspen slash accumulations reported by Perala (1974).

The five levels of fuel loading (treatments) were randomly allocated to the 50 plots, resulting in five treatments of ten replications each.

Plate 1. 0 kg/m² (0 t/ac) fuel loading. (All natural fuel removed from plot.)

Plate 2. 0.17 kg/m² (1 t/ac) fuel loading.

Plate 3. 0.87 kg/m² (5 t/ac) fuel loading.

Plate 4. 3.94 kg/m² (20 t/ac) fuel loading.

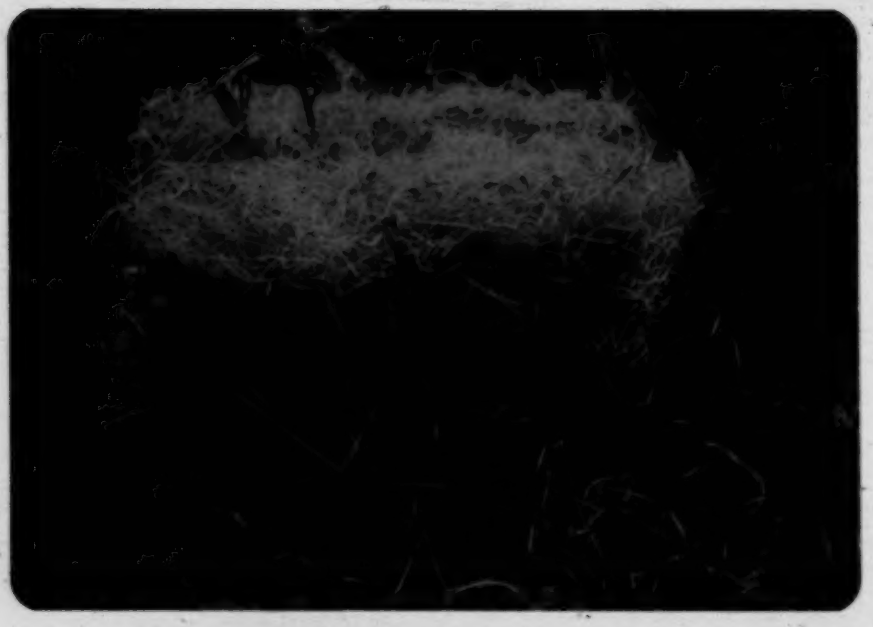

Plate 5. 9.65 kg/m² (50 t/ac) fuel loading. (Note white spruce slats inserted in center of fuelbed).

Fuel loadings were initially determined in tons/acre. These units correspond to the units used in Rothermel's (1972) fire model, which was used in calculating of packing ratios for the fuelbeds. Table 1 presents the fuel loadings chosen and their metric equivalents. Due to lack of time, the fuelbeds were constructed without having taken moisture content samples. Therefore, the original loadings (in tons/acre) are given as green weights, while the loadings listed in the kg/m^2 column are oven-dry weights.

Table 1. Selected fuel loadings in English units with metric equivalents.

tons/acre[1]	tonnes/ha[1]	kg/m^2[2]
0	0	0
1	2.2	0.17
5	11.2	0.87
20	44.8	3.94
50	112.1	9.65

[1] green weight
[2] oven-dry weight

4.3 Fuelbed Parameters

Several parameters were measured in an attempt to describe the physical arrangement of each artificial fuelbed: the available fuel loading (kg/m^2), fuelbed depth (cm), fuelbed bulk density (kg/m^3), and packing ratio, which is dimensionless. These quantities are defined in Appendix I. Table 2 summarizes these data for each fuelbed. Available fuel is defined as the amount of fuel actually consumed in a

fire (Brown and Davis 1973).

Fuel loading for each plot is expressed in kg/m^2 to enable comparisons with conventional fuel loading measurements (VanWagner 1978). Of the five levels of fuel loading chosen, 0.87 kg/m^2 corresponds most closely to the average natural fuel loading on the burn area (0.98 kg/m^2). The heaviest natural fuel loadings were estimated to be 2-4 kg/m^2, and corresponded to the 3.94 kg/m^2 fuelbed. It seems unlikely that natural fuel loadings in this fuel type would reach the fuel loadings simulated by the heaviest artificial fuelbed (9.65 kg/m^2).

Fuelbed depth is important in determining fuelbed bulk density, and also determines the height at which combustion takes place relative to the height of the target plants. The heaviest fuelbeds showed the most variation in depth as a result of inserting the white spruce slats.

Fuelbed bulk density and packing ratio are measurements of the amount of fuelbed volume occupied by solid fuel. Both parameters are important in determining residence times and levels of fire intensity (Rothermel 1972).

Total heat release (Albini 1976) was used to quantify the level of fire disturbance experienced by each target plant. Total heat release integrates energy output over the entire period of burning (Woodard 1977), and requires only simple calculations. In addition, packing ratios, which strongly affect reaction intensities, were calculated for each fuelbed (Rothermel 1972).

Table 2. Fuelbed parameters measured on each of the 50 fire disturbance plots.

Plot Number	Available fuel[1,2] (Kg/m²)	Fuelbed depth (cm)	Fuelbed bulk density (Kg/m³)	Packing ratio
1	0	--	-----	------
2	0.17	7	2.43	0.0056
3	9.59	28	34.25	0.0792
4	3.94	27	14.59	0.0337
5	0.87	13	6.69	0.0155
6	0.87	14	6.21	0.0144
7	0.17	7	2.43	0.0056
8	3.94	25	15.76	0.0364
9	9.68	32	30.25	0.0699
10	0	--	-----	------
11	0	--	-----	------
12	9.70	31	31.29	0.0723
13	0.17	8	2.13	0.0049
14	0.87	11	7.91	0.0183
15	3.94	24	16.24	0.0380
16	3.94	23	17.13	0.0396
17	9.66	33	29.27	0.0677
18	0.87	12	7.25	0.0168
19	0	--	-----	------
20	0.17	7	2.43	0.0056
21	0.87	10	8.70	0.0201
22	3.94	27	14.59	0.0337
23	9.64	32	30.13	0.0697
24	0	--	-----	------
25	0.17	7	2.43	0.0056
26	0	--	-----	------
27	9.70	30	32.33	0.0748
28	3.94	25	15.76	0.0364
29	0.87	11	7.91	0.0183
30	0.17	7	2.43	0.0056
31	0.17	7	2.43	0.0056
32	0.87	10	8.70	0.0201
33	3.94	24	16.42	0.0380
34	9.50	37	25.67	0.0594
35	0	--	-----	------
36	0	--	-----	------
37	0.17	9	1.89	0.0044
38	9.65	33	29.24	0.0676
39	3.94	25	15.76	0.0364
40	0.87	12	7.25	0.0168
41	0.87	14	6.21	0.0144
42	3.94	26	15.15	0.0350
43	9.69	35	27.68	0.0640

Table 2. (continued)

Plot Number	Available fuel[1,2] (kg/m^2)	Fuelbed depth (cm)	Fuelbed bulk density (kg/m^3)	Packing ratio
44	0	--	-----	------
45	0.17	7	2.43	0.0056
46	0.17	5	3.40	0.0079
47	0.87	14	6.21	0.0144
48	0	--	-----	------
49	3.94	27	14.59	0.0337
50	9.68	27	35.85	0.0829

Notes: [1] Available fuel is based on amount of fuel consumed by burning. Values for the heaviest fuelbeds vary due to incomplete combustion of spruce slats.
[2] A zero indicates fuel-free plots.

The effects of varying levels of fire disturbance were assessed in two different ways. Twenty-five of the 50 plots were randomly chosen for testing fire-induced plant mortality. The enzyme peroxidase is present in the photorespiratory system of living plant tissue (Bonner and Varner 1976), and a test for its presence should indicate whether the plant is alive or dead. Shearer (1975) made extensive use of this test in determining post-fire plant mortality on burned-over sites in Montana. He used a solution of 1% (by weight) of orthotolidine ((-C6H3-4NH2-3-CH3)2) in 95% methanol. This solution is sprayed on exposed cambial tissue, immediately followed by an application of USP 3% hydrogen peroxide (H2O2). These solutions react with peroxidase to form a dark-blue stain. Peroxidase denatures when plant cells are dead, and no color change occurs when these chemicals are sprayed on dead cells

(Shearer 1975). In this study, the bark was removed from the stems of burned target plants, and the chemicals applied. In addition, underground stems were excavated and sprayed to determine whether depth of mortality was affected by fire disturbance level.

The remaining 25 plots were reserved for monitoring the rate of plant recovery following burning. Wild red raspberry was common on these plots, and was included with hazel in these measurements. The location of each hazel and raspberry stem on the 60 cm x 60 cm central plot was mapped prior to the fire, which allowed each sprout to be followed throughout the growing season. Level of post-fire recovery was estimated by 1) counting the number of sprouts emerging on each plot, 2) measuring height growth of each sprout, and 3) counting the number of leaves on each sprout. Height growth was measured from the duff surface to the top of the highest growing bud. These measurements were performed at bi-weekly intervals from July 4 to August 30, 1980.

In addition to monitoring the immediate post-fire recovery of the target plants, it was also decided to measure biomass production at the end of the second growing season following the fire. Biomass was not measured during the first season due to the lack of suitable biomass regression equations for very young hazel and raspberry plants, and the destructive nature of clip-and-weigh methods. However, some measure of the effect of the fire treatments on shrub productivity was desired, so the 50 fire

disturbance plots were harvested 15 months following the fire. The entire aboveground portions of the hazel and raspberry plants were clipped, transported to the laboratory, dried for approximately 120 hours at 75°C, and weighed.

Analysis of the fire disturbance data was carried out using a one-way analysis of variance and subsequent multiple comparisons test. Using the BMDP1V Analysis of Variance computer program (Dixon and Brown 1979). Analysis of variance was performed separately for number of sprouts, height growth, and number of leaves produced by each sprout, and was carried out separately for each measurement date. The hypothesis tested was that there were no differences between means of the response variables over the different fire disturbance levels.

4.4 Regenerative Mechanisms

The second objective of this study was to determine the type and relative importance of the various regenerative mechanisms utilized in post-fire plant re-establishment. To achieve this objective, 30 cm x 30 cm duff cores extending down to mineral soil were removed and transported to the greenhouse. A total of 100 duff cores were removed, one prior to and one subsequent to burning from each of the 50 fire disturbance plots (Fig. 5). Pre-burn cores were removed one day before the fire and the post-burn cores were removed

the week following the fire. This resulted in 50 paired cores, and enabled the direct comparison of pre- and post-burn plant recovery on a plot by plot basis.

The duff cores were placed in the University of Alberta greenhouse under ambient (summer) light conditions and watered as necessary. The greenhouse environment eliminated losses due to predation and post-fire micro climatic effects which may have inhibited natural regeneration. Seedlings and sprouts were identified, classified as to origin, and immediately removed to prevent interplant competition.

4.5 Prescribed Fire

4.5.1 Natural Fuel Documentation

Natural fuels present on the burn site were also documented. Litter and grass fuels predominated, and were measured by clipping, drying and weighing ten 0.1m² plots located throughout the study site. Down and dead woody fuels did not contribute significantly to the fuel complex. Moisture content of the litter, grass and live and dead woody fuels was gravimetrically determined daily for four days prior to burning. These data allowed a determination of the moisture trends for all size class fuels prior to burning.

Characteristics of the organic soil layer were also documented. Duff (F and H layer) reduction due to burning

was assessed using 't-bar' survey pins (McRae et al. 1979). The pins were positioned so that the cross bar was level with the surface of the duff. Amount of duff reduction was determined by measuring the distance from the cross bar to the surface of the duff following burning. A 't-bar' pin was placed midway along each side of the 2 m x 2 m plots (see Fig. 5). Other duff characteristics were also measured. Duff depth was measured on all 50 plots, and 32 duff samples were removed for laboratory determination of moisture content. Duff moisture content was determined by weighing the moist samples, drying them for 24 hours at 75°C, and reweighing. Moisture content was expressed as a percentage of oven-dry weight.

An attempt was also made to develop a regression equation relating duff weight to duff depth. Fifty undisturbed soil samples were removed from the burn site using a soil sampling cylinder with a diameter of 7.5 cm. Each sample extended into mineral soil to ensure that all organic matter was collected. After each sample was removed, the thickness of the F and H layers was measured twice along opposing sides of the sampling hole. The samples were individually sealed in plastic bags and transported to the laboratory. The samples were then oven-dried for 48 hours at 75°C and weighed.

The weight of the organic matter was determined using loss-on-ignition, as modified from Ball(1964). Each sample was ground until homogeneous, and a smaller subsample taken.

The subsamples were then weighed and placed in a muffle furnace at 600°C for 12-16 hours. After heating, the subsamples were again weighed, the percent organic matter calculated, and the organic matter content of the original sample determined. The weight of the organic matter was then converted to kg/ha and regressed against duff depth using the BMDP1R Multiple Linear Regression computer program (Dixon and Brown 1979). Only 35 samples were used in the regression analysis due to damage to the samples during transportation and oven-drying.

4.5.2 Fire Control Methods

Traditional methods of control in prescribed burning operations have included the construction of a mineral soil fire-line around the perimeter of the burn area (Brown and Davis 1973). In a park setting however, impacts of firebreak construction should be held to a minimum. Disturbance of vegetation and soil adversely affects aesthetic values, and may lead to soil erosion.

To overcome the difficulties associated with fire-line construction, a new approach has been taken at Elk Island National Park. Containment of prescribed burns is accomplished by using a "wet line". First, a 1.5 meter wide swath was cut through the understory vegetation along the boundary of the burn area. A firehose was then laid along the swath, and 50 cm high industrial sprinklers inserted in the hoseline at 30 meter intervals. Water pumps were

installed at both ends of the hose line, and drew water from the lake on the east side of the burn area. The pumps were started approximately three hours prior to ignition. The sprinklers have an effective watering range of about 15 meters. Using this approach, the fire was successfully contained without extensive site disturbance. Figure 6 shows the layout of the control line.

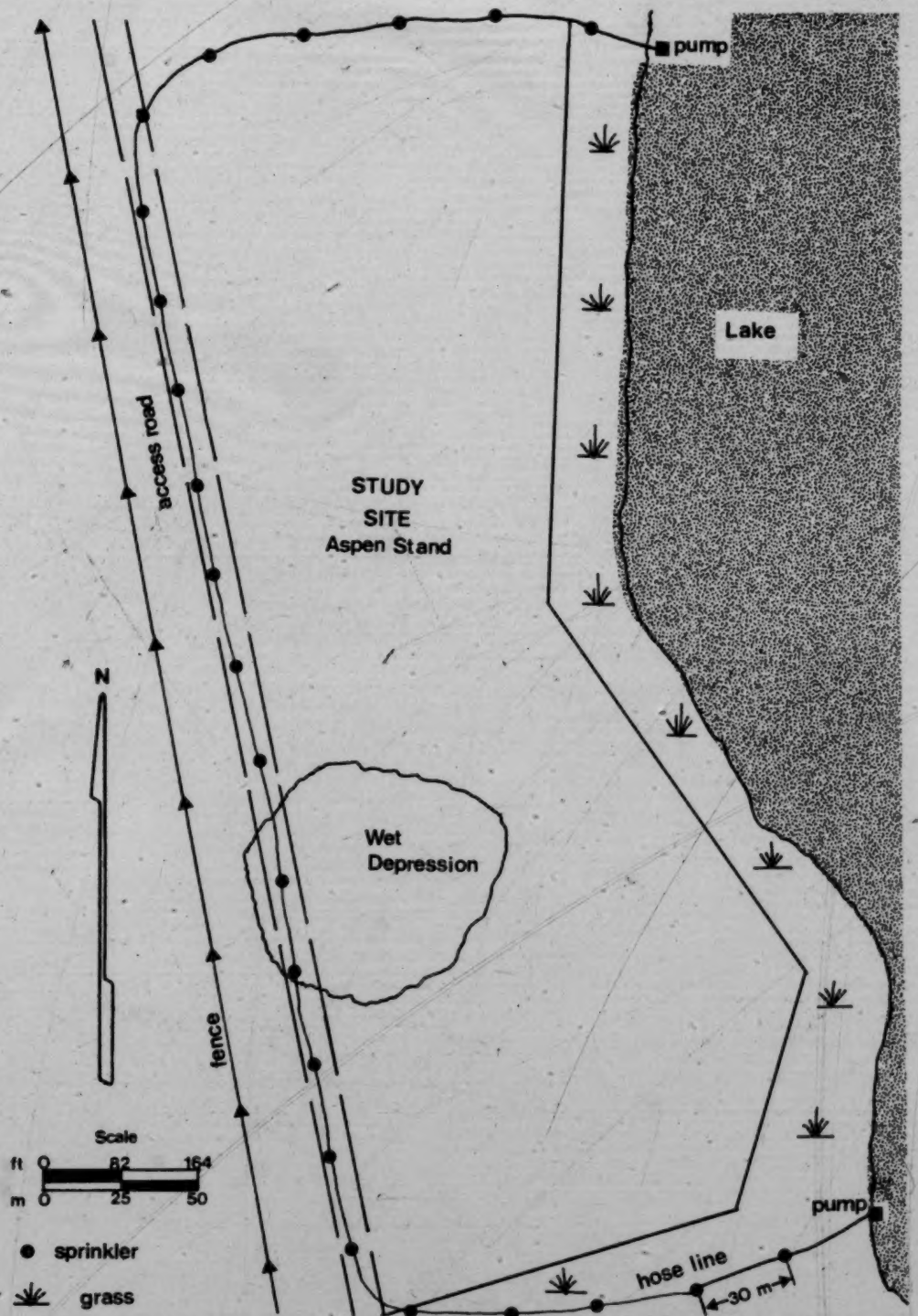

Figure 6. Control line layout used for Elk Island prescribed burn, 5 May, 1980.

5. RESULTS

This chapter is divided into two major sections: The Prescribed Fire and Postburn Effects. The first section pertains to the prescribed fire carried out for this study, and includes fuel loading data, weather and Forest Fire Weather Index data, and a description of the ignition pattern used and the fire behavior observed. The second section includes the post-fire effects on the target plants as revealed by the orthotolidine test and the measurement of recovery rates. This section also includes the results of the greenhouse bioassay study.

5.1 The Prescribed Fire

5.1.1 Natural Fuel Loading

Naturally occurring fuels on the burn area were documented. The average fuel loading on the site was 0.98 kg/m^2, but varied considerably over the entire burn area. Aspen litter predominated under the canopy, and produced loadings of 0.4 to 1.5 kg/m^2. Grass fuels were more important in open areas, and the loadings were somewhat lower (0.3 to 0.9 kg/m^2). The heaviest natural fuel loadings occurred along the edge of the lake, where moist conditions produced heavy grass growth. Fuel loadings here were estimated at 2.0 to 4.0 kg/m^2.

In contrast to coniferous forest stands, the aspen forest fuel complex consisted primarily of dried herbaceous stems and aspen leaf litter. Dead and down roundwood fuels made up a negligible portion of the fuel loading. The lack of woody fuel has important implications in predicting fire behavior and fire effects in these stands. Fire behavior in these stands would be characterized by rapid rates of spread and short residence times, due to the flashy nature of the fine fuels. Fire moves quickly between fuel particles, but the small size and relatively low heat contents of the fine fuels prevent major impacts on the site. In addition, these fuels are highly flammable in spring before green-up. At this time, the duff (F and H layers) moisture is usually still high, and only the litter (L) layer will burn (Bailey and Anderson 1980). High duff moisture contents retard heat penetration into the deeper duff layers which results in little or no impact to underground reproductive organs (VanWagner 1972).

Shrubby fuels contributed to the fuel complex as well. Bailey and Anderson (1980) found that dense stands of western snowberry (Symphoricarpos occidentalis) and willow (Salix sp.) contributed large amounts of fuel on a prescribed burning site in east-central Alberta. In the present study, wild gooseberry (Ribes hirtellum) added large amounts of fuel in isolated spots, but did not contribute to the forward spread of the fire.

The results of the duff weight/depth study indicated that the "best fit" regression equation was:

$$Y = 24.25 + 3.08\ X \qquad (5)$$

where: Y = duff weight, kg/ha
X = duff depth, cm

Figure 7 presents a graph of the regression equation. Analysis of variance of the regression (Table 3) indicates that the relationship is significant ($p=0.00002$); duff weight is positively correlated with duff depth. However, the r^2 value is low ($r^2=0.4239$), indicating that the regression only accounts for 42% of the observed variability.

Disturbance by animals affected the physical arrangement of the fuel complex. Breaks in the horizontal fuel continuity were caused by ungulate trails, which occurred throughout the burn site. Trails were up to one meter wide, and had significant effects on the spread of the fire. Grazing virtually eliminated the grass from some of the open areas, thus completely removing fuel. Shrub height was greatly reduced as a result of browsing, which in turn reduced the available fuel and the potential for crown fires.

Fuel moisture is also important in determining fire behavior (Schroeder and Buck 1970). Fuel moisture trends were documented for all fuel size classes for the four days prior to the fire. Table 4 summarizes the moisture trends

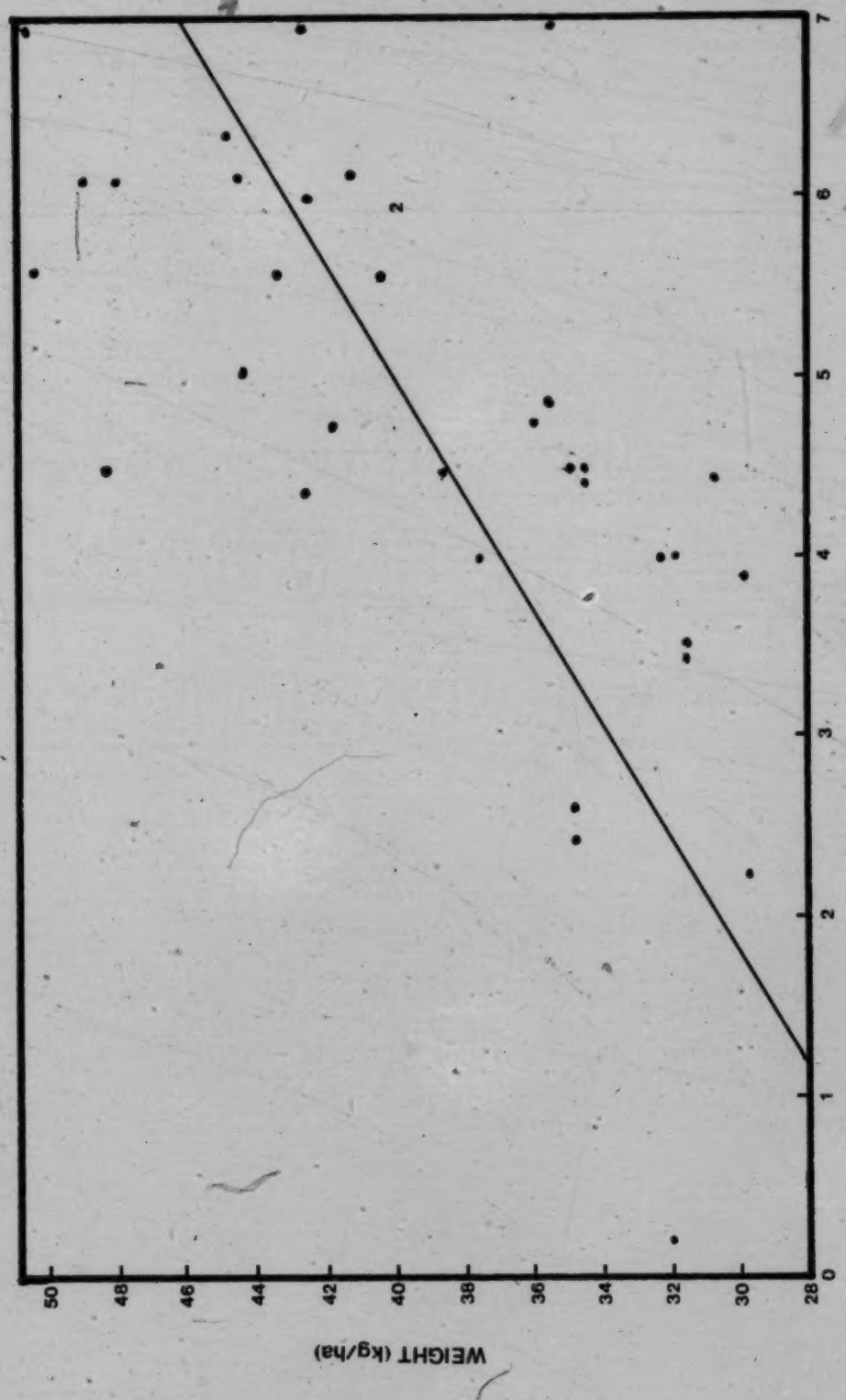

Figure 7. Relationship between duff weight and duff depth in an aspen forest (n=35 samples).

Table 3. Statistical information pertaining to the regression equation relating duff weight to duff depth.

DATA SUMMARY

VARIABLE	MEAN	STANDARD DEV.	COEFFICIENT OF VARIATION	MINIMUM	MAXIMUM
DUFF DEPTH (cm)	4.77142	1.39296	0.29194	1.00000	7.00000
DUFF WEIGHT(kg/ha)	38.92955	6.58120	0.16906	29.85516	53.03307.

REGRESSION OF DUFF WEIGHT V.S. DUFF DEPTH

r = 0.6511
r squared = 0.4239
STD. ERROR OF EST. = 5.0704

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	624.210	1	624.210	24.280	0.00002
RESIDUAL	848.403	33	25.709		

VARIABLE	COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT	24.25258					
DEPTH	3.07602	0.624	0.651	4.927	0.000	1.00000

for each class.

Table 4. Moisture content by each fuel type and size class (% ovendry weight).

Fuel size class	2 May	3 May	4 May	5 May*
leaf litter	12.5	24.2	11.6	15.5
grass (dead)	10.0	5.1	7.4	13.4
0-0.60 cm (dead)	19.0	21.5	9.8	12.4
0.60-2.5 cm (dead)	6.6	13.5	9.6	9.9
2.5-7.6 cm (dead)	--	11.2	9.6	12.6
7.6+ cm (dead)	11.3	--	17.2	--
0-0.60 cm (live)	120.0	152.0	178.1	169.1
0.60-2.5 cm (live)	80.0	105.0	150.2	118.1

* Date of prescribed burn

The only precipitation experienced between snowmelt and the date of the prescribed burn was 1.96 mm of rain that fell the night of 2 May[3]. The precipitation is reflected in the higher fuel moisture contents of 3 May. The dead grass fuel was the only fuel type which did not seem to respond to the rainfall.

The moisture content of the artificial fuelbeds was determined on the day of the burn only. The moisture content of the excelsior was 12.0%, and the moisture content of the white spruce slats was 17.9%. Both values are expressed as percent of oven-dry weight.

Duff moisture content was also determined on the day of the burn. Thirty-two duff samples were removed from randomly

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[3] Unpublished weather records on file at Elk Island National Park.

chosen plots throughout the burn area. Mean duff moisture content was 121.3% ± 31.7%, oven-dry weight.

5.1.2 Weather Conditions and Forest Fire Weather Index

Weather conditions during a prescribed burn are a very important factor in determining fire behavior (Brown and Davis 1973). Precipitation adds moisture to fuels, humidity and wind speed determine drying rates and rates of spread, and air temperature determines the amount of heating necessary to raise plant tissue to lethal levels (Schroeder and Buck 1970). The relative influence of all these factors is integrated in the Canadian Forest Fire Weather Index (FFWI) (VanWagner 1974).

The moisture codes of the FFWI represent the moisture contents of three types of fuel: litter and other fine fuels (Fine Fuel Moisture Code), loosely compacted organic matter (Duff Moisture Code), and deep, compact organic matter (Drought Code). These codes account for the wetting and drying behavior of these fuels and are cumulative over the fire season. The Fine Fuel Moisture Code is combined with wind speed to yield an estimate of the rate of spread of a fire in fine fuels (Initial Spread Index). The Duff Moisture Code and the Drought Code are combined to form an index representing the total fuel available to a spreading fire (Buildup Index). Finally, the Initial Spread Index and the Buildup Index combine to form the Fire Weather Index, an estimate of the intensity of a spreading fire expressed as

energy output per unit length of fire front (VanWagner 1974).

Table 5 presents the weather observations and FFWI data for the date of the prescribed burn (5 May, 1980). Also included in Table 5 are weather and FFWI values recommended by Dube (1979) for prescribed burning in Elk Island National Park. The weather and FFWI values recorded for the day of the burn correspond fairly well with those suggested by Dube (1979), but are somewhat less than optimum. The fire behavior observed in the present study was characterized by low rates of spread, short flame length, and little crown damage. The burning conditions recommended by Dube (1979) are conducive to somewhat more intense fire behavior, but still may not result in extensive site damage. If the goal of the burn was to reduce shrub cover or kill aspen trees, the fire intensities reached would probably be insufficient.

Table 5. Weather and FFWI data for Elk Island prescribed burn (1400 hrs, 5 May, 1980) and optimum weather conditions suggested by Dube (1979).

	Observed	Dube (1979)
Temperature	12°C	16-23°C
Windspeed	6 kph	15-25 kph (max)
Relative Humidity	33%	20-35%
Fine Fuel Moisture Code	87	85-95
Duff Moisture Code	58	
Drought Code	239	
Initial Spread Index	4	5-12
Buildup Index	72	>20
Fire Weather Index	14	10-20

5.1.3 Ignition and Fire Behavior

The initial prescription for the burn called for a west wind and the use of the lake on the east side of the burn as the principal firebreak. However, the wind was from the east on the day of the burn, which resulted in a modification of the planned ignition sequence.

The first step in the ignition sequence was to backfire a 2 meter wide safety strip inside the sprinkler line. The backfire was begun at the southwest corner of the area and proceeded north along the sprinkler line (see Fig. 6). At the north end of the burn area, the backfire was continued east to the edge of the lake. When the backfire strip had burned out, ignition proceeded south along the edge of the lake.

The resulting headfire spread rapidly up the embankment and into the aspen stand. Heavy dry grass accumulations along the edge of the lake produced rapid rates of spread, but the fire slowed considerably upon entering the aspen stand. Lower fuel loadings and higher humidity under the canopy caused a dramatic reduction in rate of fire spread and flame lengths. Table 6 presents the extremes in fire behavior observed in the various fuel types on the burn area.

Table 6. Extremes in fire behavior observed during the Elk Island prescribed burn.

Fuel Type	Flame Length (m)	Rate of Spread (m/min)	Fireline Intensity (kW/m)
aspen litter	0.10-0.15	0.25-0.50	40-80
litter/grass	0.15-0.30	0.5	100-150
heavy grass	5-8	10-15	6,000-18,600

The heavy fuel accumulations along the lake edge created the most severe fire behavior on the burn site. Long flame lengths and rapid rates of spread make this a hazardous fuel type in which to burn if proper precautions are not taken. However, damage to the site was minimal due to the short residence times and the moist soil conditions.

Fire behavior was much less intense under the aspen canopy, due to the lower fuel loading and more compact fuelbed. Only the trees along the edge of the lake experienced any crown damage. The foliage of most of the shrubs on the burn area was scorched or consumed, and some shrubs experienced complete consumption of aboveground stems. Wild gooseberry (Ribes hirtellum) was particularly important in influencing fire behavior. This species adds new growth in concentric circles around the original stem. As the new growth accumulates, the older central stems die and create a compact mass of extremely flammable fuel. As the fire spread to these shrubs, the central portion burned furiously. Both the dead stems and the live green stems were consumed, leaving only a clump of burned stubs. Nearly all

of the R. hirtellum shrubs were consumed in this manner.

Natural fuel consumption on the burn area was limited to dried grass and aspen leaf litter. Due to low moisture contents and favorable fuel arrangements, consumption of these fuels was nearly complete. Some areas of grass fuel remained unburned due to heavy grazing, and high duff moisture contents prevented consumption of the F and H soil layers.

Fuel consumption in the artificial fuelbeds was nearly complete due to favorable packing ratios and low moisture contents. The excelsior burned completely, leaving only a small amount of ash residue. The only portion of the artificial fuelbeds not totally consumed was the white spruce slats embedded in the heaviest (9.65 kg/m^2) fuelbeds. None of these slats were completely consumed, and the unburned portions accounted for approximately 3% of the total fuelbed weight. Incomplete combustion may have been due to higher moisture contents (17.9% vs 12.0% for the excelsior) or lack of sufficient residence time due to rapid consumption of the excelsior.

Duff consumption was nil. Approximately 130 pins were distributed throughout the burn area, and none showed any evidence of duff consumption. Lack of duff consumption was attributed to the high duff moisture content (121.3%).

Forty-three of the 50 artificial fuelbeds were consumed in the prescribed burn, which prevented the direct observation of their fire behavior. The remaining seven

fuelbeds were not ignited by the fire due to poor continuity of natural fuels and were subsequently ignited using matches. The fire behavior in these fuelbeds was documented and is presented in Table 7.

Table 7. Fire behavior data observed for the seven fuelbeds ignited with matches.

Plot Number	Fuel Loading (kg/m^2)	Flame Length (m)	Residence Time (min)
6	0.87	1.12	2.0
17	9.65	1.62	10.0
18	0.87	1.12	2.0
30	0.17	0.27	1.5
33	3.94	1.55	4.0
43	9.65	2.32	10.0
49	3.94	1.55	4.0

Figure 8 presents a graphical display of the flame length data, and also includes a graph of Byram's (1959) expression relating flame length to fireline intensity.

The curve relating I_B to flame length (Byram 1959) agrees fairly well with the flame lengths observed on the lower fuel loadings (0.17, 0.87 and 3.94 kg/m^2). Both curves represent a rapid increase in flame length with increasing fuel weight. However, the curves begin to diverge at the higher fuel loading (9.65 kg/m^2). This lack of agreement may be due to the lack of sufficient observations (2), or the fact that white spruce slats were added to the heavier fuelbeds. The lower surface area to volume ratios and higher residence times of these fuelbeds may have caused lower combustion rates and consequent lower flame lengths. In

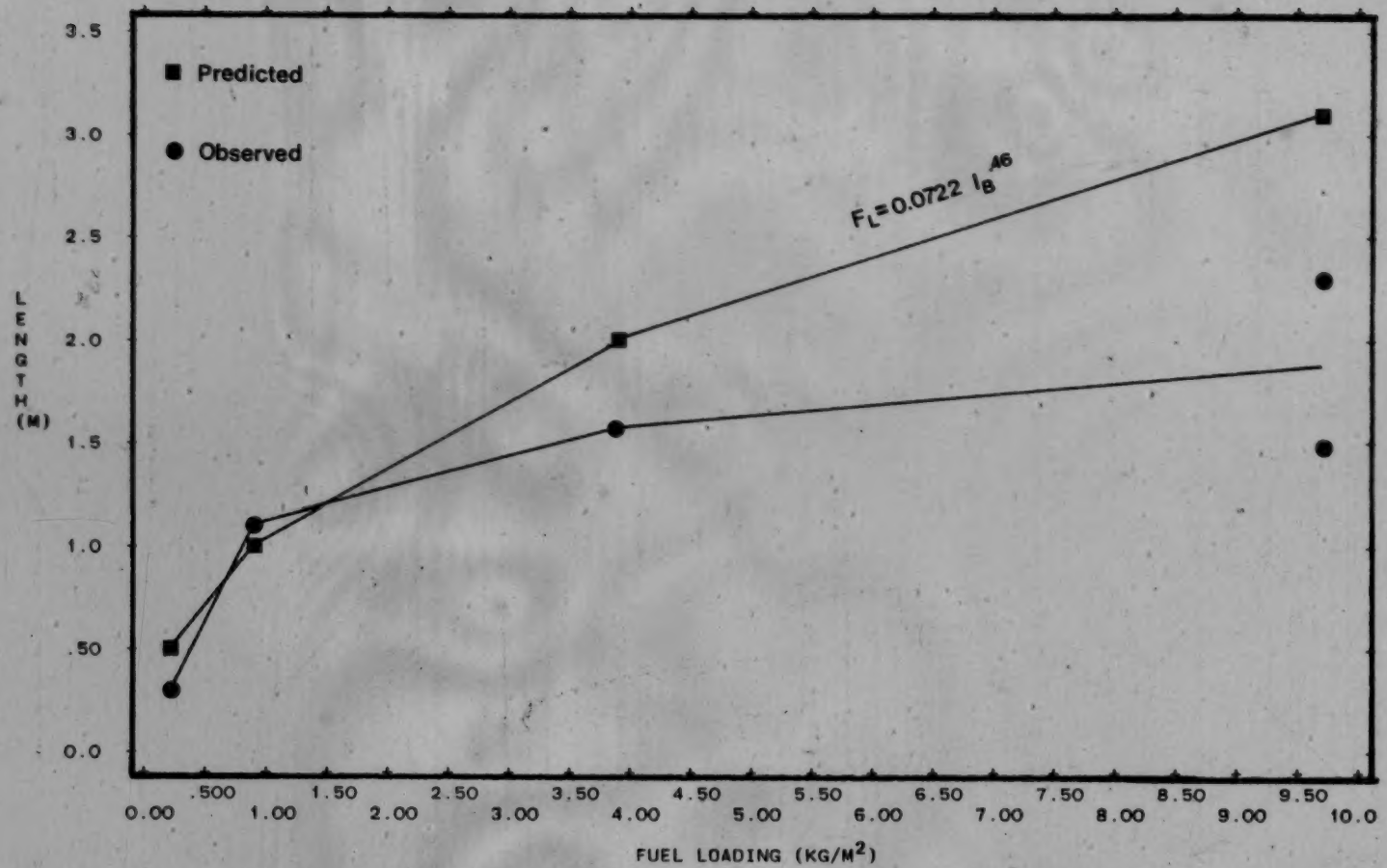

Figure 8. Flame lengths (F_L) observed for each artificial fuel loading and flame lengths calculated from Byram's (1959) equation using a calculated fireline intensity (I_B).

addition, Byram's (1959) relationship was developed for use in homogeneous fuelbeds that have reached steady-state burning conditions (Rothermel and Deeming 1980). The 9.65 kg/m^2 fuelbeds consisted of two different sizes of fuel (excelsior and spruce slats), and may have been too small for combustion to reach steady-state conditions.

Residence time is the length of time flaming combustion continued in each fuelbed (Rothermel and Deeming 1980). The first three fuel loadings (0.17, 0.87 and 3.94 kg/m^2) demonstrate a linear increase in residence time with increasing fuel weight (Fig. 9). However, the 9.65 kg/m^2 fuelbeds show a disproportionate increase in residence time. This is probably due to the addition of white spruce slats to these fuelbeds. The slats increased the amount of solid fuel within the fuelbed, creating more available fuel and increasing the packing ratio. Therefore, residence times were increased (Rothermel 1972).

Total heat release (Albini 1976) was used to quantify the amount of heat flux experienced by the target plants. Total heat release is the product of the heat of combustion of the fuel and the weight of fuel consumed. Table 8 presents these data for each plot. Values for heaviest fuel loadings vary due to incomplete combustion of the spruce slats. Total heat release was calculated by multiplying the available fuel X the heat of combustion for white spruce (18,600 kJ/kg, Appendix I).

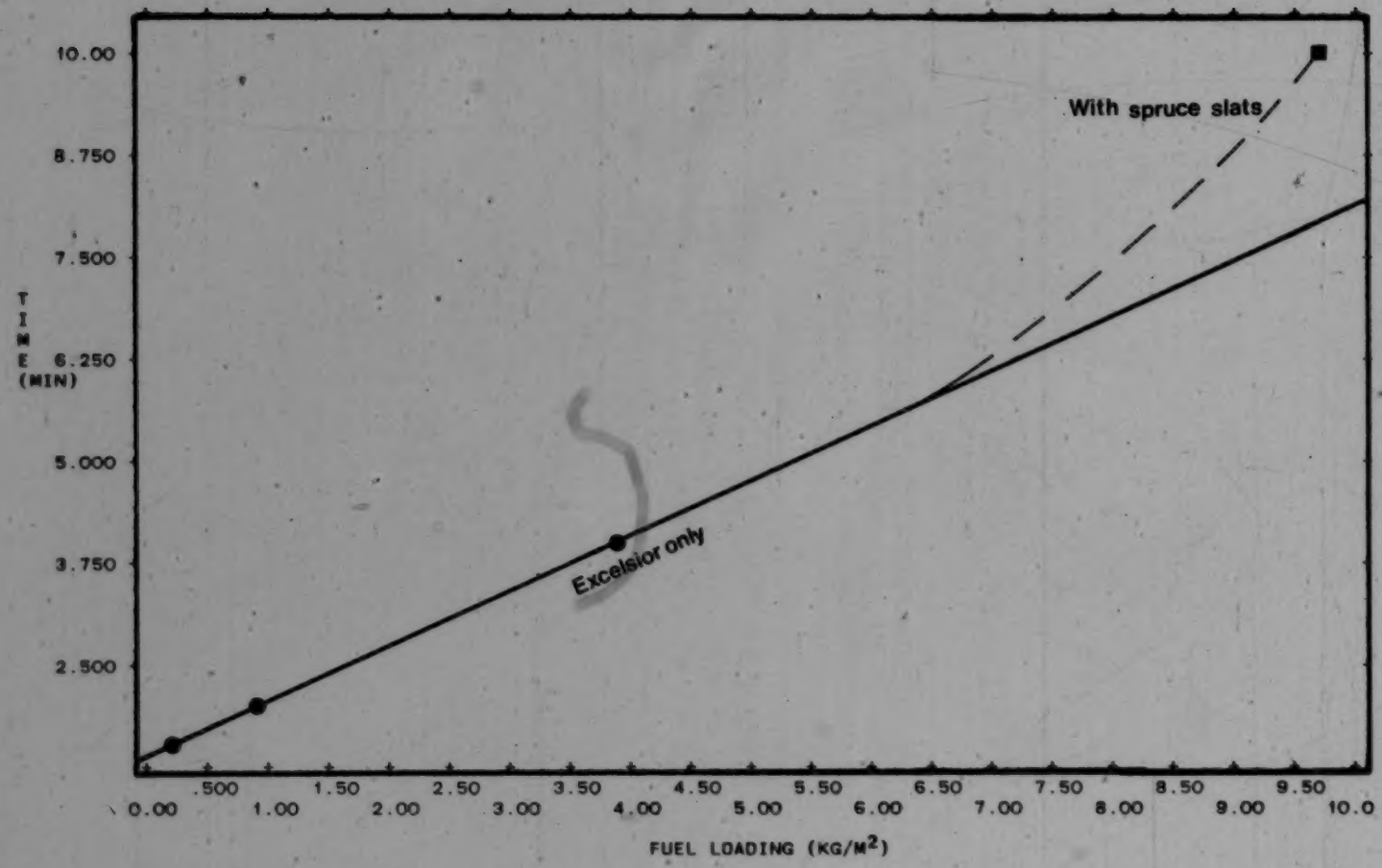

Figure 9. Residence times observed for each artificial fuel loading.

Total heat release varied widely between plots, from 3217 kJ/m² to 180,439 kJ/m². Natural fuel accumulations are unlikely to produce as broad a range in heat output. The average fuel loading on this site (1 kg/m²) would produce a total heat output of about 18,600 kJ/m²; the heaviest natural fuel loading observed (4 kg/m²) would produce a total heat output of 74,000 kJ/m². This latter value is approximately equal to the 3.94 kg/m² fuelbed. The highest total heat release reached (180,439 kJ/m²) is unlikely to occur in this fuel type except under very severe burning conditions and extraordinary fuel accumulations (e.g. blowdown or logging slash). The range of total heat release produced by the artificial fuelbeds seemed to include all conditions likely to be encountered in this fuel type.

Table 8. Fuel consumption and total heat release for each of the 50 fire disturbance plots.

Plot number	Fuel consumed[1] (kg)	Total heat release (kJ/m²)
1	0--[2]	----0
2	0.06	3,217
3	3.45	178,429
4	1.42	73,284
5	0.31	16,144
6	0.31	16,144
7	0.06	3,117
8	1.42	73,284
9	3.49	180,141
10	0---	------0
11	0---	------0
12	3.49	180,364
13	0.06	3,217
14	0.31	16,144
15	1.42	73,284
16	1.42	73,284
17	3.48	179,713
18	0.31	16,144
19	0---	------0
20	0.06	3,217
21	0.31	16,144
22	1.42	73,284
23	3.47	179,322
24	0---	------0
25	0.06	3,217
26	0---	------0
27	3.49	180,439
28	1.42	73,284
29	0.31	16,144
30	0.06	3,217
31	0.06	3,217
32	0.31	16,144
33	1.42	73,284
34	3.42	176,662
35	0---	------0
36	0---	------0
37	0.06	3,217
38	3.47	179,416
39	1.42	73,284
40	0.31	16,144
41	0.31	16,144
42	1.42	73,284
43	3.49	180,308

Table 8. (continued)

Plot number	Fuel consumed (kg)	Total heat release (kJ/m²)
44	0---	------0
45	0.06	3,217
46	0.06	3,217
47	0.31	16,144
48	0---	------0
49	1:42	73,284
50	3.49	180,104

[1] Fuel consumed was calculated by multiplying available fuel (kg/m²) by the area of the artificial fuelbed (0.36 m²).

[2] Plots on which no fuel was added.

5.2 Postburn Effects

5.2.1 Orthotolidine Test

Above-ground plant mortality was uniform over all plots on which fuel was added as determined by the orthotolidine test (Shearer 1975). All plant tissue exposed to heat on these plots was killed. Some mortality even occurred on the fuel-free plots as well. Heat transfer by radiation and convection was sufficient to expose cambial tissue on these plots to lethal temperatures, in spite of the absence of fuel adjacent to the plant stems. However, due to non-uniform heat transfer, some portions of stems on the fuel-free plots remained alive. In addition, all foliage on all plots was consumed. Figure 10 presents a diagram of the

observed fire effects.

Below-ground plant mortality was also tested using the orthotolidine test. Mortality extended slightly below the surface of the duff on some plots with higher fuel loadings, but there were not enough of these plots to enable a statistical analysis. The results of the orthotolidine test on all other plots indicated that mortality did not occur below the duff surface. Table 9 presents the fuel loading and depth of mortality for all plots on which mortality extended below the duff surface.

Table 9. Artificial fuel loading and depth of mortality on plots experiencing below-ground mortality.

Plot number	Fuel loading (Kg/m^2)	Depth of mortality (cm)
8	3.94	2.0
15	3.94	2.0
42	3.94	1.5
9	9.65	1.0
27	9.65	3.0
33	9.65	2.0
43	9.65	2.0

Although plots experiencing below-ground mortality were too few to produce statistically significant results, the above data do suggest that the heavier fuel loadings may produce some heat penetration into the duff. However, the depths of mortality reached are probably not deep enough to significantly affect post-fire shrub resprouting. The underground stems of hazel and raspberry both occur deeper than the measured depth of heat penetration, based on

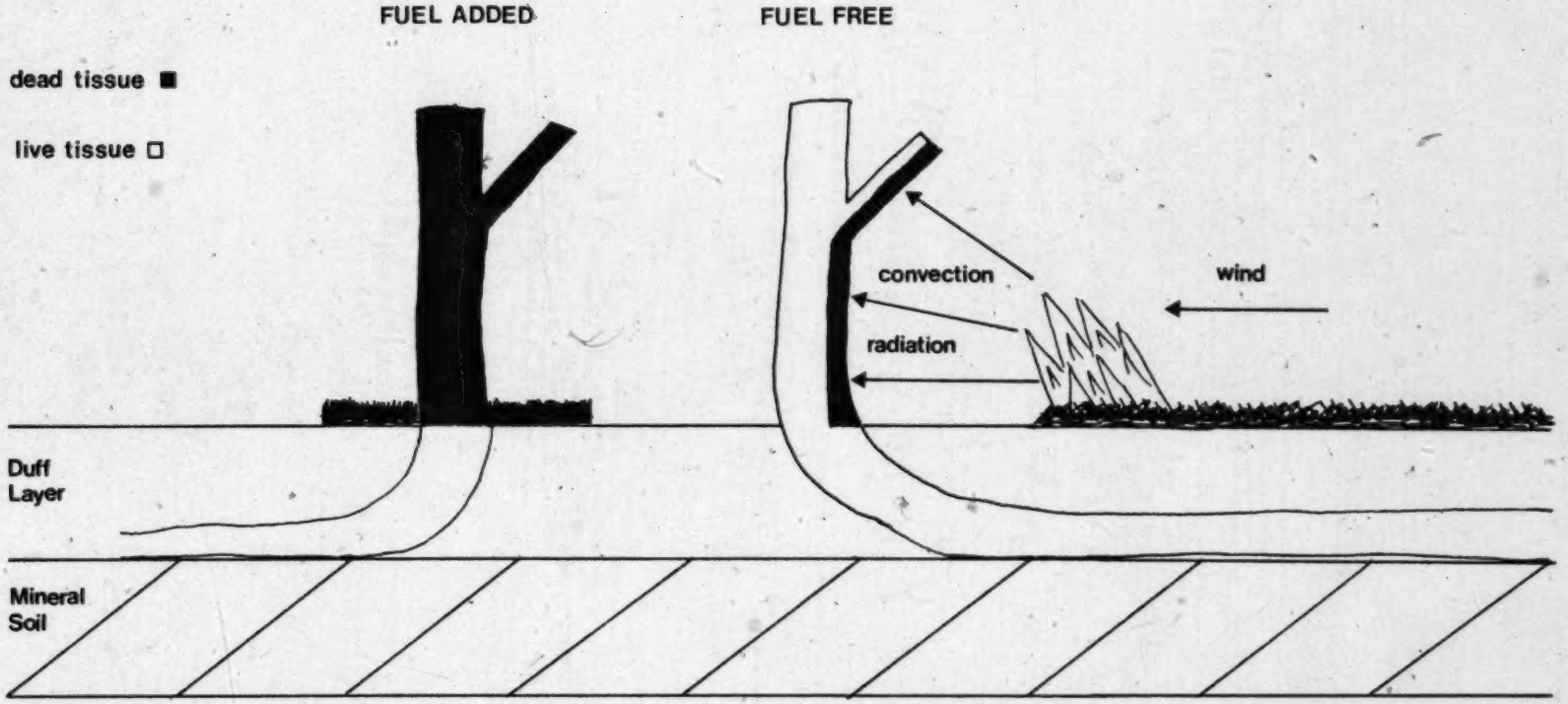

Figure 10. Diagram of effects of fire on shrub stems as determined by the orthotolidine test.

observations made during this study. Underground hazel stems usually occurred from 5-10 cm below the duff surface, while raspberry stems were from 0-5 cm below the duff surface.

5.2.2 Recovery Rates

An initial examination of the recovery rate data indicated that a significant number of sprouts (up to 50% on some plots) experienced a reduction in height growth and number of leaves between successive measurement dates following burning. The cause of these losses was not directly observed, nor was the cause discernable by observing the plants on which it occurred. Several explanations were considered, including browsing by moose or other ungulates (LaRoi pers. comm)[4], plant shrinkage, soil subsidence, insect herbivory and others. However, none of these agents were directly observed. In addition, the plots on which the disturbance occurred were equally distributed over the entire study site, which seems to preclude a localized disturbance such as browsing or some environmental effect (shading, allelopathy, etc.). In order to prevent the presence of this secondary disturbance from confounding the statistical analysis, the data were divided into "disturbed" and "undisturbed" subpopulations and analyzed separately.

Tables 10-13 present the mean values for number of sprouts, height growth, and number of leaves for each

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[4]G.H. LaRoi. Department of Botany, University of Alberta. Personal communication, 1980.

measurement date and treatment. Number of sprouts is the same for both disturbed and undisturbed subpopulations.

One-way analysis of variance and subsequent multiple comparison tests indicated that the most frequent difference between treatments was between the fuel-free treatment and the other fuel loadings combined. The addition of fuel in any amount often caused a significant decline in height growth and number of leaves. If comparisons between the fuel-free treatment and all of the other treatments are not considered, only 27 of approximately 500 comparisons indicate significant differences between treatments. All comparisons were considered significant if $p \leq 0.05$.

Table 10 presents the recovery data for undisturbed hazel stems. Number of sprouts is not significantly different between any of the treatments on any of the dates. Height growth is significantly different, but only between the fuel free treatment and the other treatments. Number of leaves is significantly different for the first three dates only. July 4 is the only date on which the differences are significant between the added fuel treatments. Significant differences are between the 0.17 kg/m^2 and the 0.87 and 3.94 kg/m^2 treatments. All plants in the fuel-free treatment were placed in the disturbed subpopulation because all showed a reduction in height and number of leaves.

Table 10. Recovery rate data for undisturbed hazel sprouts, 1980.

DATE	Fuel loading (kg/m²) 0	0.17	0.87	3.94	9.65	
July 4	8	17	4.5	6	3	s[1]
	66.4a[2]	14.8b	13.2b	7.8b	6.4b	h
	-[3]	5 a	4 a,b	4 a	3 b	l
July 22	7	17	5	7	8	s
	68.6a	20.7b	15.9b	15.0b	19.4b	h
	-	6 a	4 a	5 a	6 a	l
August 1	6	18	5	8	7	s
	68.6a	21.4b	15.9b	15.7b	19.6b	h
	-	6 a	5 a	4 a	7 a	l
August 16	6	18	5	7	7	s
	69.8a	21.7b	16.1b	22.3b	19.6b	h
	-	6 a	5 a	5 a	6 a	l
August 30	6	15	5	7	8	s
	69.8a	21.8b	15.9b	21.7b	20.0b	h
	-	5 a	8 a	5 a	6 a	l

[1] s = number of sprouts, h = height growth (cm) l = number of leaves per sprout.

[2] Values followed by similar letters in a row not significantly different ($p \leq 0.05$).

[3] Indicates that no undisturbed plants occurred in this treatment as indicated by number of leaves.

Table 11 presents the recovery rate data for the disturbed hazel stems. As with previous data, the most frequent difference was between the fuel-free treatment and all of the other treatments. Number of sprouts is not significantly different in any case. Height growth is significantly different between the various added fuel treatments on July 4, August 1 and August 16; the number of

Table 11. Recovery rate data for disturbed hazel sprouts, 1980.

DATE	Fuel loading (kg/m²) 0	0.17	0.87	3.94	9.65	
July 4	8	17	5	6	3	s[1]
	61.3a[2]	26.4b	25.0b	9.8c	11.8c	h
	24 a	5 b	6 b	4 b	3 b	l
July 22	7	17	5	7	8	s
	62.1a	32.8b	32.1b	19.4b	24.5b	h
	24 a	7 b	8 b	5 b	5 b	l
August 1	6	18	5	8	7	s
	56.6a	29.1b,c,e	26.6b,c,d,e	14.0c,d,e	27.8b,c,d,e	h
	19 a	4 b	4 b	3 b	6 b	l
August 16	6	18	5	7	7	s
	57.8a	28.3b	27.7b	13.5c	28.8b	h
	19 a	3 b	3 b	3 b	7 b	l
August 30	6	15	5	7	8	s
	58.2a	27.8b	27.7b	13.8b	25.0b	h
	18 a	3 b	3 b	2 b	3 b	l

[1] s = average number of sprouts/plot h = height growth (cm)
l = number of leaves/sprout

[2] values followed by similar letters in a row not significantly different ($p \leq 0.05$).

leaves is different on all dates only between the fuel-free treatment and all the other treatments. It should be kept in mind that the difference in recovery rates between treatments may have been substantially affected by the additional disturbance.

Table 12 provides the recovery rate data for undisturbed raspberry stems. Height growth is significantly different on all dates. The differences in all cases are between the fuel-free treatments and the other treatments, and between the 0.17 kg/m^2 and the three higher disturbance level treatments. Number of leaves showed the greatest number of significant differences between treatments. Significant differences in number of leaves occurred on the first three measurement dates only. Significant differences on July 4 are between the fuel-free treatments and all others; between 0.17 kg/m^2 and 0, 3.94 and 9.65 kg/m^2; and between 0.87 and 0 and 9.65 kg/m^2. Differences on July 22 and August 1 were between the fuel-free treatment and all others, and between 0.17 kg/m^2 and all others. Here again, all plants in the fuel-free treatment were placed in the disturbed subpopulation.

Table 13 presents the recovery rate data for disturbed raspberry stems. No significant differences in number of sprouts, height growth, or number of leaves occurred between any of the treatments on any of the measurement dates.

Figures 11-15 present recovery rate growth curves for the four subpopulations. In general, a similar pattern is

Table 12. Recovery rate data for undisturbed raspberry sprouts, 1980.

DATE	Fuel loading (kg/m²) 0	0.17	0.87	3.94	9.65	
July 4	5 52.0a[2] -[3]	4 32.7b 8 a,b	4 17.4b,c 6 a,b	4 12.2b,c 5 b,	5 8.8b,c 3	s[1] h l
July 22	6 58.8a -	4 36.5b 9 a,b	5 19.5b,c 7 a,b	4 16.1b,c 6 b	7 12.8b,c 5 b	s h l
August 1	3 58.4a -	4 36.8b 8 a	4 19.1b,c 6 a	4 16.2b,c 5 a	7 13.5b,c 5 a	s h l
August 16	3 60. a -	4 37.2b 7 a	5 21.0b,c 7 a	4 16.7b,c 6 a	7 13.5b,c 6 a	s h l
August 30	3 60.2a -	2 37.0b 7 a	4 20.8b,c 6 a	3 16.8b,c 5 a	7 13.8b,c 6 a	s h l

[1] s = average number of sprouts/plot
h = height growth (cm)
l = number of leaves/sprout

[2] Values followed by similar letters in a row not significantly different ($p \leq 0.05$).

[3] Indicates that no undisturbed plants occurred in this treatment as indicated by number of leaves.

Table 13. Recovery rate data for disturbed raspberry sprouts, 1980.

DATE	Fuel loading (kg/m²) 0	0.17	0.87	3.94	9.65	
July 4	5	4	4	4	5	s[1]
	42.7	17.0	19.2	11.0	25.0	h
	18	6	10	5	6	l
July 22	6	4	5	4	7	s
	41.7	20.0	23.4	15.7	34.0	h
	18	7	11	5	8	l
August 1	3	4	4	4	7	s
	35.3	18.3	20.6	14.3	38.0	h
	14	9	10	3	7	l
August 16	3	4	5	4	7	s
	37.3	19.3	22.6	16.3	36.0	h
	12	5	7	10	10	l
August 30	3	2	4	3	7	s
	40.3	19.0	22.2	15.3	36.0	h
	10	8	8	8	7	l

[1] s = average number of sprouts/plot
h = height growth (cm)
l = number of leaves/sprout.

evident in the growth curves and in the analysis of variance tables; that is the most frequent differences between recovery rates were between the fuel-free treatment and the other added-fuel treatments. The growth curves also indicate the onset of the additional disturbance. Height growth declined between July 22 and August 7 on nearly all of the disturbed plots, and did not seem to occur again through the remainder of the growing season.

5.2.3 Shrub Biomass

Results of the shrub biomass measurements taken at the end of the second growing season indicate that, similar to the recovery rate data, the only major difference between treatments was between the fuel-free plots and all of the other treatments. As shown in Table 14, hazel biomass was significantly greater on the fuel-free plots than on the 0.17, 0.87,3.94 and 9.65 kg/m^2 plots. Even at the end of two growing seasons, this difference is still apparent.

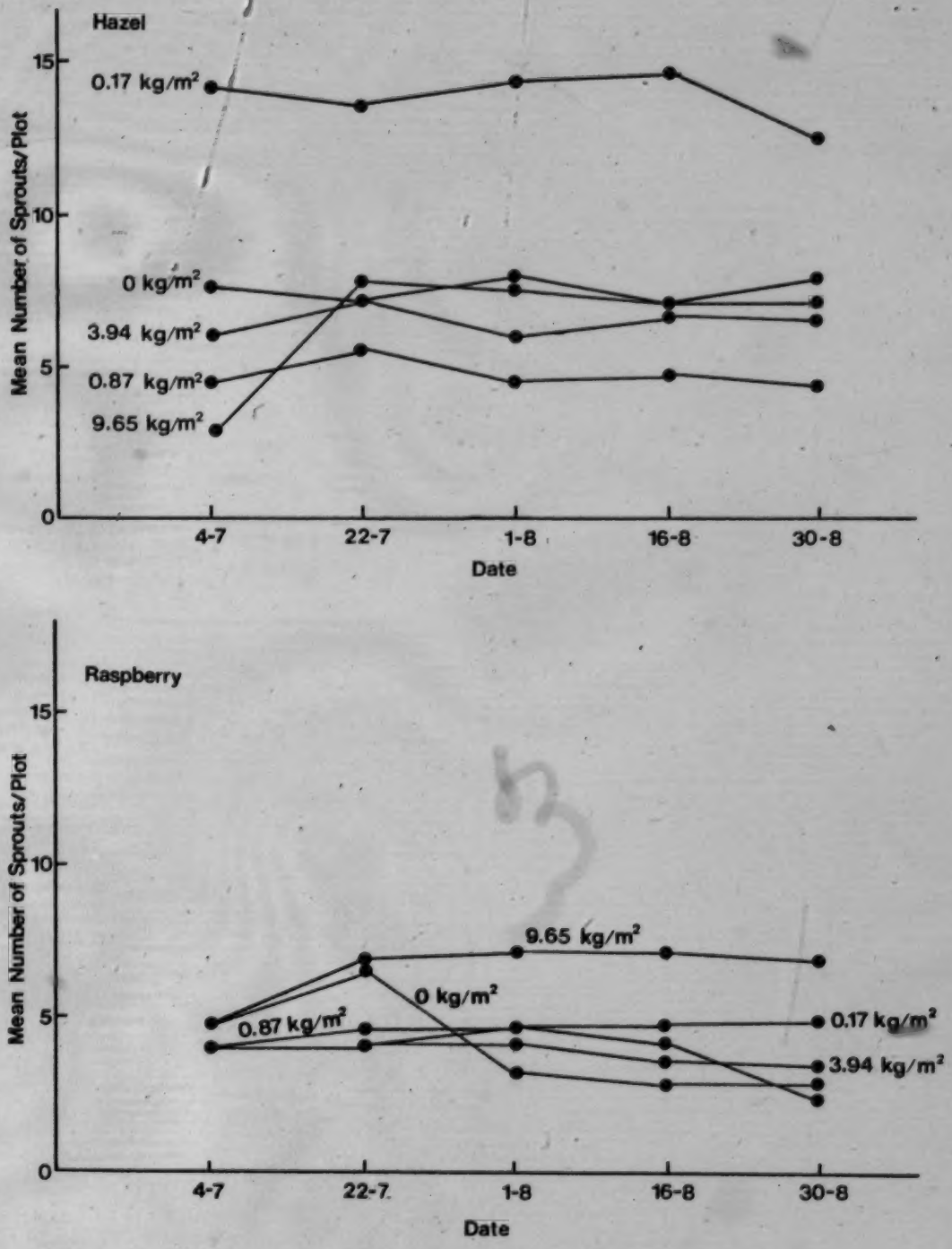

Figure 11. Number of sprouts produced for each fire disturbance level. Hazel (upper), raspberry (lower). 1980.

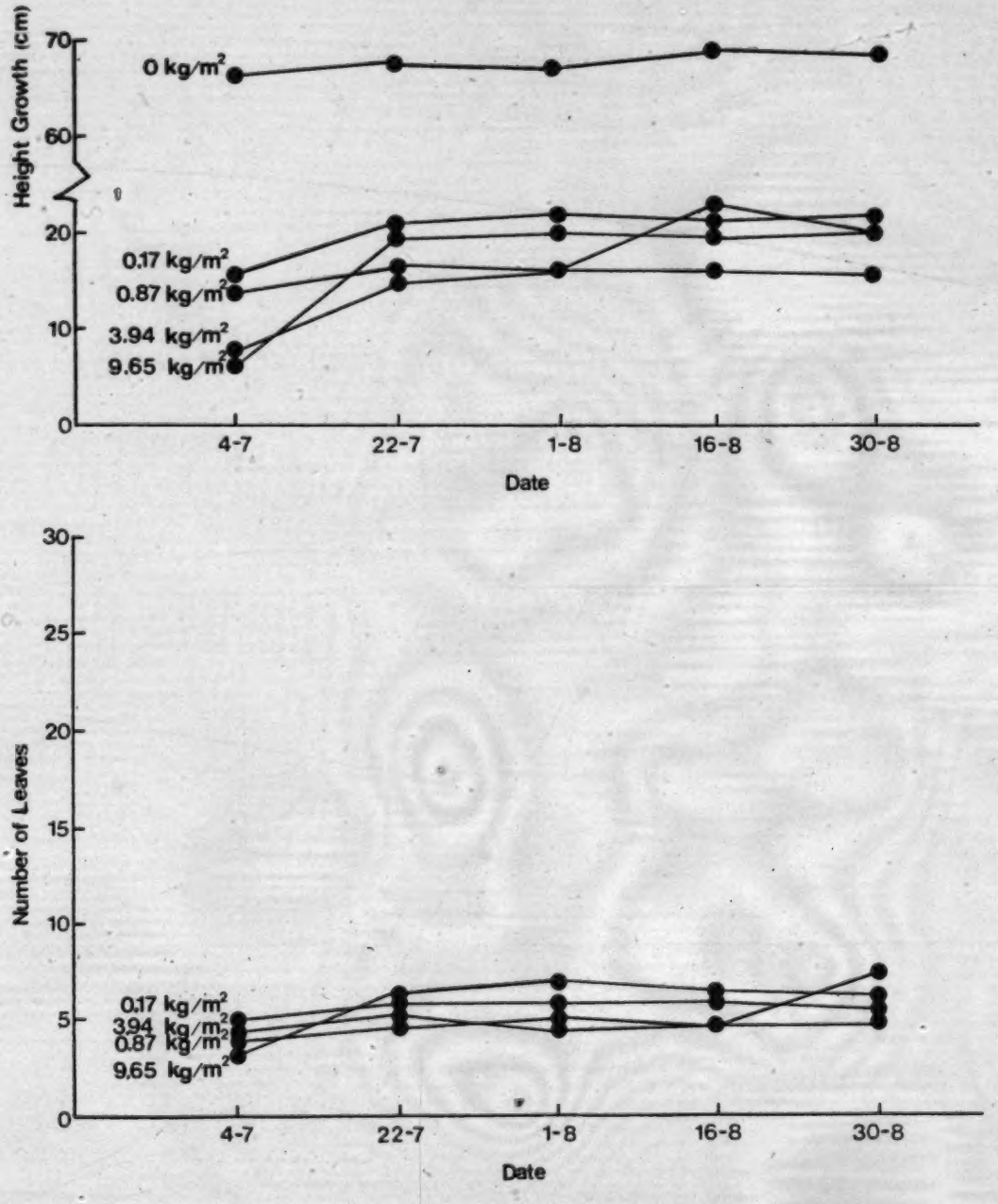

Figure 12. Recovery rate data for undisturbed hazel stems for each fire disturbance level. Height growth (upper), number of leaves (lower). 1980.

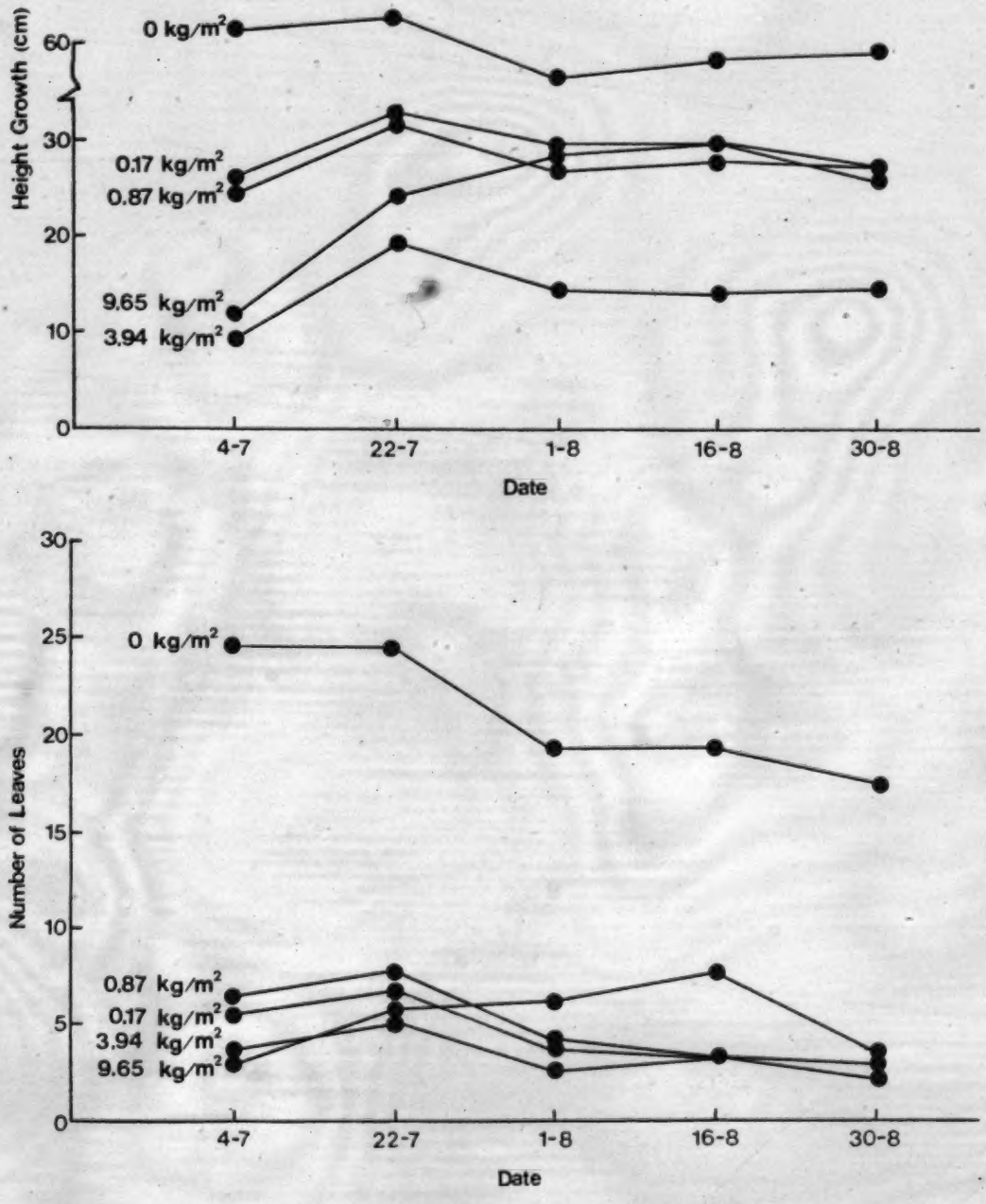

Figure 13. Recovery rate data for disturbed hazel stems for each fire disturbance level. Height growth (upper), number of leaves (lower). 1980.

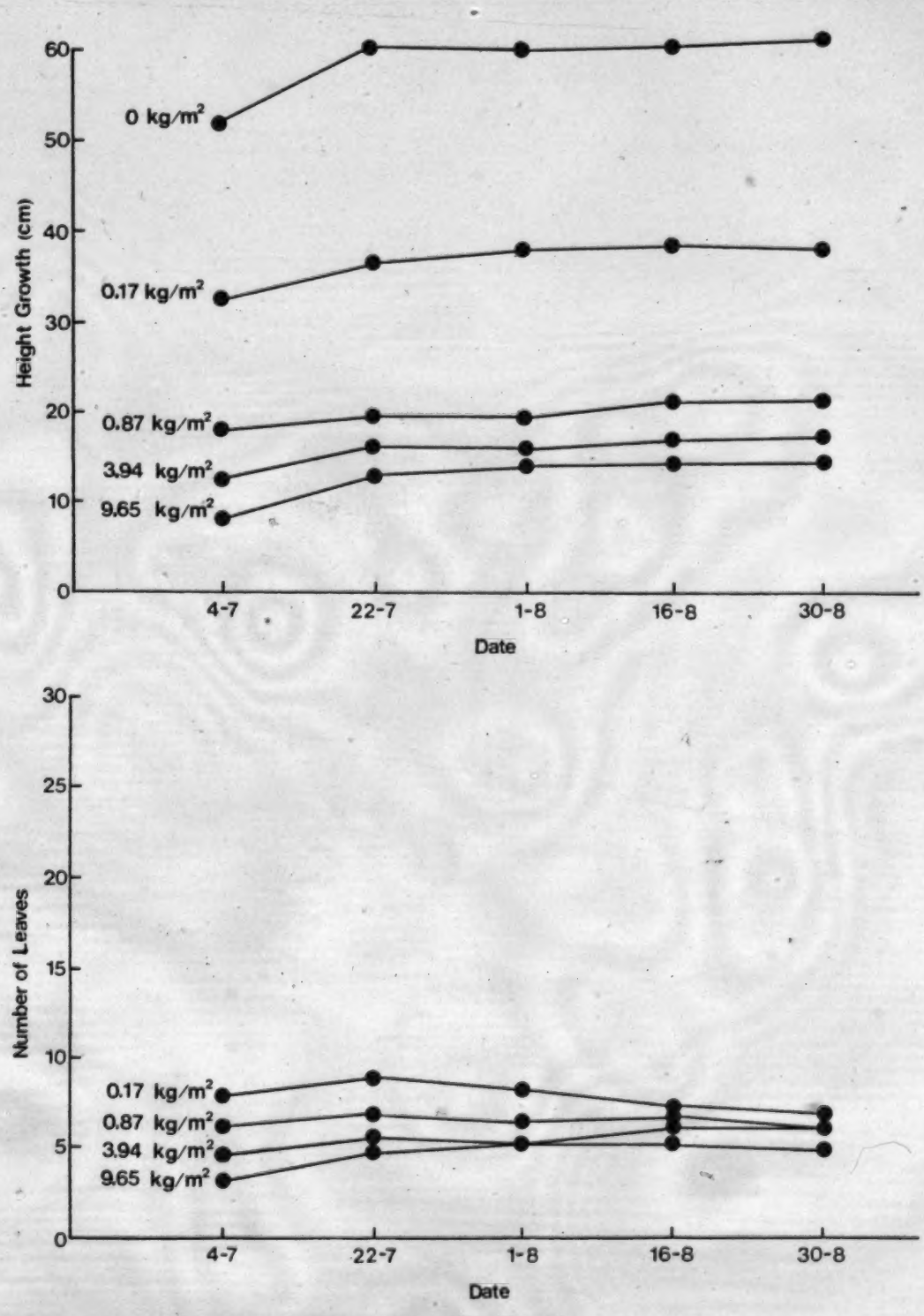

Figure 14. Recovery rate data for undisturbed raspberry stems for each fire disturbance level. Height growth (upper), number of leaves (lower). 1980.

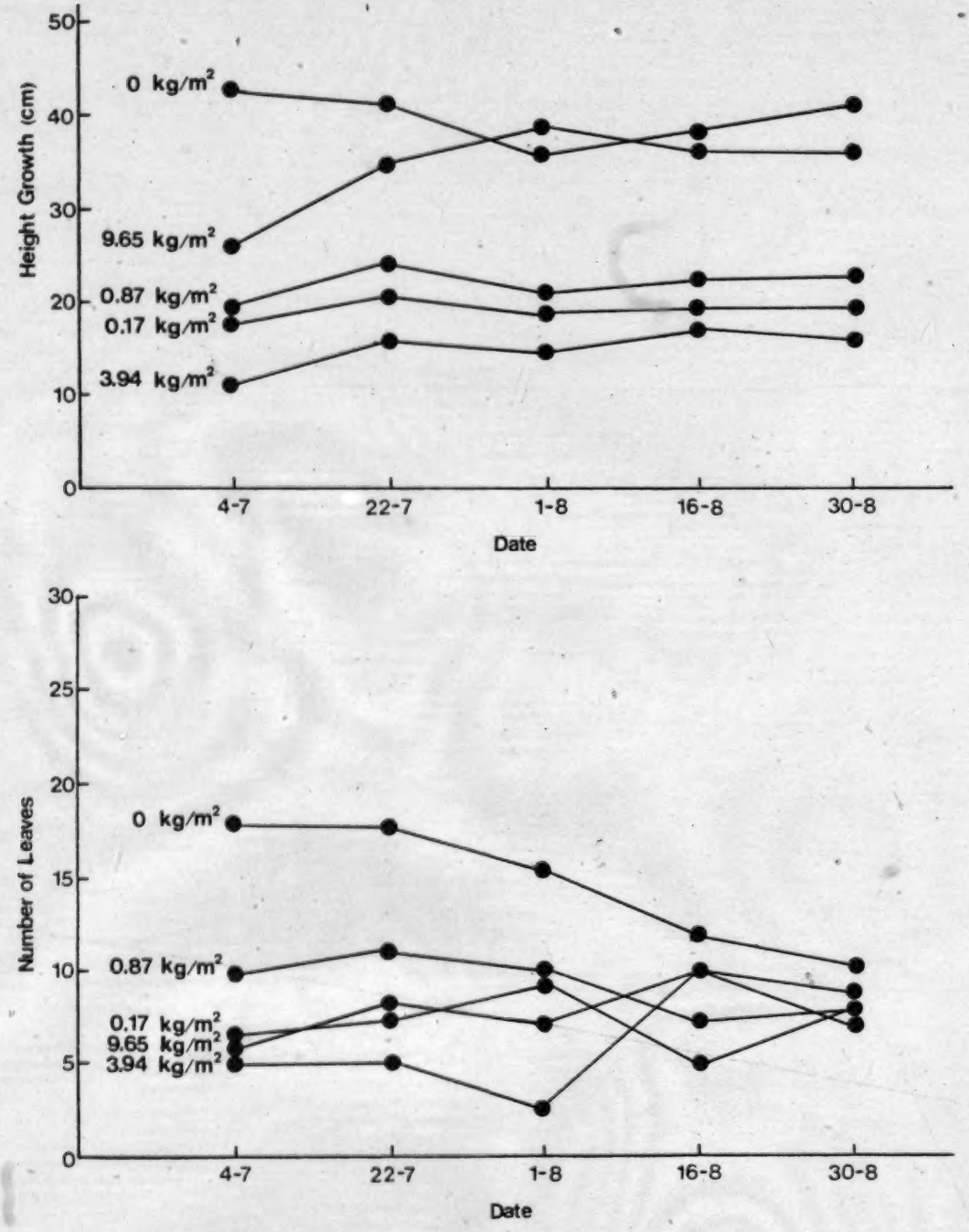

Figure 15. Recovery rate data for disturbed raspberry stems for each fire disturbance level. Height growth (upper), number of leaves (lower). 1980.

Table 14. Mean above-ground biomass (gms) of hazel and raspberry shrubs for each treatment 15 months following burning.

	Fuel loading (kg/m^2)				
	0	0.17	0.87	3.94	9.65
hazel	59.89 a[1]	14.66 b	11.37 b	8.51 b	9.79 b
raspberry	2.48 a	4.14 a	5.05 a	4.59 a	4.36a

[1]Values followed by similar letters in a row not significantly different ($p \leq 0.05$).

Raspberry biomass measurements reveal a different response to burning. On these plots, there were no differences between any of the treatments; biomass was not significantly different in any case.

5.2.4 Greenhouse Bioassay Study

The second major objective of this study was to identify and quantify those methods of reproduction important in plant re-establishment following burning. Paired pre-and post-burn duff cores were removed from each of the 50 plots on the burn site. The cores were transported to the University of Alberta greenhouse and placed under optimum growing conditions.

Twenty-five of the 35 species emerging from the duff cores were restricted to either seed or vegetative reproduction (Table 15), and both were equally represented (13 seed and 12 vegetative). Ten species originated from

Table 15. Percent frequency of occurrence of plants originating from seed and vegetative means on burned and unburned cores (n = 50).

	SEED		VEGETATIVE		Primary mode of reproduction[2]
	unburned	burned	unburned	burned	
Achillea millefolium	2	0			S
Anemone canadensis	0	6	0	4	S+V
Apocynum androsaemifolium	0	2			S
Aralia nudicaulis			16	18	V
Aster sp.			10a	4b	V
Chenopodium album	4	2			S
Chenopodium hybridum var. gigantospermum	0	2			S
Cirsium arvense	26	24			S
Cornus canadensis			4	4	V
Crepis runcinata	0	4			S
Epilobium angustifolium			2	2	V
Erigeron acris	38a[1]	10b	34	46	S+V
Fragaria virginiana	52a	26b	16	24	S(V)
Galium boreale	20a	46b	26	8	S+V
Galium triflorum	0	2	2	2	S+V
Geranium viscosissimum	2a	16b	0	2	S(V)
Geum allepicum var. strictum	20a	38b			S
Labiateae	8	12			S
Lathyrus ochroleucus			46a	28b	V
Maianthemum canadense			20	12	V
Mitella nuda	4	0	4	4	S+V
Plantago major	50a	24b			S
Potentilla sp.			6a	2b	V
Rosa acicularis			2	0	V
Rubus pubescens			10	10	V
Rubus strigosus	34	40	28	26	S+V
Sanicula marilandica			2	2	V
Solidago decumbens	10	0			S
Symphoricarpos albus			10	12	V
Taraxacum officinale		38	2	0	S(V)
Thlaspi arvense	2	0			S
Trifolium repens	14	20			S
Urtica gracilis	32	36			S
Vicia americana			44	38	V
Viola rugulosa	2	0	28	22	V(S)

Notes: [1] Pairs of values followed by different letters are significantly different ($p \leq 0.05$)

[2] Primary mode of reproduction: s=seed, v=vegetative. Letter in parentheses indicates secondary importance:

Totals: S = 13, V = 12, S+V = 6, S(V) = 3, V(S) = 1

both sources. Of these ten, six were equally represented by seed and vegetatively produced plants, three were primarily from seed with some vegetatively produced plants, and one was primarily of vegetative origin with a small number of seed produced plants.

A chi-square test was used to test for differences in percent frequency of occurrence of each species between burned and unburned cores. Table 16 presents these data.

Table 16. Species originating primarily on burned or unburned duff cores, based on chi-square test ($p \leq 0.05$).

Seed Origin	
Erigeron acris	unburned*
Fragaria virginiana	unburned
Galium boreale	unburned
Geranium viscosissimum	burned*
Geum allepicum	burned
Plantago major	unburned
Vegetative Origin	
Aster sp.	unburned
Galium boreale	unburned
Lathyrus ochroleucus	unburned
Potentilla sp.	unburned

* unburned = significantly greater number of plants occurred on unburned cores.
* burned = significantly greater number of plants occurred on burned cores.

Six species originating from seed demonstrated significant differences between burned and unburned cores: Erigeron acris, Fragaria virginiana, Galium boreale, Geranium viscosissimum, Geum allepicum and Plantago major. Of these species, E. acris, F. virginiana, Galium boreale and P. major each had significantly fewer germinants on the burned cores, and seemed to be adversely affected by burning. Geranium viscosissimum and Geum allepicum seem to be stimulated by burning, with significantly more germinants on the burned cores.

Four species of vegetative origin showed significant differences between the burned and unburned cores: Aster sp., G. boreale, Lathyrus ochroleucus and Potentilla sp. In all cases, the frequency of occurrence was greater on unburned cores. These species seemed to be adversely affected by burning as well. It is interesting to note that Galium boreale is represented by seedlings and sprouts, which are both adversely affected by burning. In this case, method of reproduction seems to make no difference in the response of this species to fire.

The remaining 25 species showed no differences between burned and unburned cores.

The greenhouse bioassay data was also analysed by comparing total species richness (number of species) between all burned and unburned cores. A Mann-Whitney U-test was used to test for significant differences in mean number of species on the burned and unburned cores. Mean number of

species on the burned and unburned cores were not significantly different for either vegetative or seed produced plants; all cores produced an average of three species.

In addition to the 50 pre- and post-burn duff cores, duff samples were taken from locations that experienced extreme levels of fire disturbance. These locations were usually under downed tree boles or adjacent to stumps where fuel accumulations were very high and the fire burned for long periods of time. These samples were also placed under optimum greenhouse conditions. Six such cores were removed; a total of two plants became established on them. One was a vegetatively produced Rubus strigosus sprout, and the other was a Geranium viscosissimum seedling. This was the only indication in the entire study that high levels of fire disturbance were reached during the burn.

6. Discussion

6.1 Orthotolidine Test

The initial assumption concerning plant tissue mortality due to burning was that the target plants would experience different degrees of mortality depending on the level of fire disturbance. Therefore, it was surprising to observe that nearly all above-ground plant tissues were killed when subjected to all levels of fire disturbance. Mortality even extended to those plants that had no fuel packed around them. Lethal temperatures were achieved through convective and radiative heat transfer; direct contact with flames was not necessary. These observations indicate that the above-ground portion of the target plants is very sensitive to heating and would probably be killed by fires of any intensity.

Conversely, below-ground tissue mortality was nearly absent. Lethal temperatures penetrated 1-3 cm into the duff on some plots, but the majority of target plants experienced no below-ground mortality. As mentioned previously, the high duff moisture content was probably responsible for protecting the underground plant parts. Fuel loadings far in excess of those occurring naturally (9.65 kg/m^2) were still insufficient to generate lethal temperatures in the lower duff layers on most plots. In addition, weather conditions prior to the prescribed burn were among the driest on record

for Elk Island National Park. Less than 2 mm of rain had fallen since snowmelt, and air temperatures of 25-30°C were common two to three weeks prior to burning.[5] These conditions were certainly extreme for this area and this time of year, and yet the duff was still moist enough to fully protect the underground portions of the target plants.

The high duff moisture content in the face of extremely dry weather conditions raises the question of whether conditions would ever occur in spring in boreal aspen stands which would result in fires severe enough to kill the underground portions of resprouting shrubs. Based on the observations made in this study, it seems unlikely. Conditions may never become dry enough in spring to allow extensive mortality following burning. The only conditions under which sufficiently intense fire behavior may occur is heavy accumulations of large diameter woody fuels (aspen trees). However, due to the multi-aged structure of the aspen stand on the study site, this is unlikely to happen. A more common process in these stands seems to be a tree by tree replacement sequence, with suckering aspen reproduction replacing individual older trees as they fall. In addition, rapid rates of decomposition on these mesic sites reduce the accumulation of woody fuels.[6]

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[5] Unpublished weather records on file at Elk Island National Park, Alberta.
[6] G.H. LaRoi Botany Department, University of Alberta. Personal communication, 1980.

These observations also raise the question of the historical presence of fire in these stands. Kjorlien (1977) reports that the area including the park experienced frequent fires in the past, and was entirely burned over in 1895. Yet, if large fires are unlikely to occur in these fuel types, how were these fires supported? Apparently the vegetation is much different now than it was prior to the large fires of the late 1800's.

White spruce was a significant component of the forest vegetation prior to the 1895 fire. A recent study (Vance 1979) has investigated the paleoecology of the Elk Island National Park area, based on lake bottom cores taken from the park. Results of this study indicate that white spruce has been present in the area for thousands of years. The frequency of fire in the area was lower prior to settlement (Kjorlien 1977), and white spruce was probably present in greater numbers then due to less frequent disturbance. As settlement occurred during the late 1800's, the incidence of fires increased (Kjorlien 1977) and the area including the park was eventually burned over in 1895. The fire was probably severe enough to eliminate almost all of the existing white spruce; remnants survived only in protected areas along the lake shores and on the islands in Astotin Lake (Polster and Watson 1979). Due to the small numbers of surviving spruce, the present seed source is insufficient to allow the re-establishment of white spruce on the areas burned in the past. As a result, aspen is replacing itself

on these sites, creating areas much more resistant to burning than the former spruce-dominated sites.

6.2 Recovery Rates

The most consistent result obtained from the hazel recovery data was the differences between the fuel-free treatment and the other added fuel treatments. Of a total of 250 comparisons, 76 indicated significant differences in recovery rates between the no-fuel and added-fuel treatments, but only four of these demonstrated differences between the other disturbance levels as well.

Height growth in particular showed large differences between the 0 kg/m^2 plots and the other treatments (0.17, 0.87, 3.94, and 9.65 kg/m^2). However, these large differences may be due to the measurement techniques involved as well as the fuel treatments. The fuel-free plots did experience some fire-induced mortality, but due to non-uniform rates of heat transfer from the surrounding fuel, some portions of each plant remained alive (Fig. 10). In some cases, these unburned portions often occurred in the upper shrub canopy and acted as sites for new sprout production. Since height growth was measured from the duff surface to the top of the highest growing bud, the height measured for the sprouts on the fuel-free plots may have been overestimated. If this factor is taken into account, there may be no actual difference in hazel height growth

between any of the treatments. Number of leaves per stem was not confounded by this factor, as all foliage was consumed on all the target plants regardless of fuel loading.

The number of hazel sprouts did not differ significantly between any of the treatments. Rates of recovery did vary, but the amount of re-establishment (i.e. number of sprouts) was the same. This seems to indicate that the effect of burning on hazel re-establishment is not to reduce the number of sprouts produced, but instead to reduce the rate of growth following burning.

Number of leaves on the undisturbed plants showed significant differences between treatments on the first three measurement dates only. It may be that differences which were apparent immediately following burning became masked as other impacts on the plants occurred. Natural leaf fall, mortality due to competition, and different growth rates may become more important in the months following burning. The direct effects of the fire may not persist through the first growing season, particularly if the fire was not severe enough to damage important underground perennating organs. In addition, the secondary disturbance observed in this study may have masked other effects of burning.

Rates of recovery on the plots with the heaviest fuel loading rapidly caught up with those on the less severely burned plots (Figs. 11-15). In particular, height growth of the hazel sprouts on the heaviest fuel loading plots (Figs.

12 and 13) increased dramatically in relation to growth rates on the other treatment plots. In addition, the most severely burned plots did not seem to experience as much secondary disturbance as the other plots. This may be because the more severe burning treatments prevented the sprouts from growing tall enough to be available for browsing when the animals were present, if browsing by ungulates is accepted as the explanation for the reduced height growth. The burning treatment retarded the growth rate initially, and these sprouts were thus spared. They were then able to rapidly reach growth rates equal to those on the other plots.

The raspberry plants demonstrated a different pattern of recovery. None of the plants on the disturbed plots showed differences between treatments, either in height growth or number of leaves. This may be another case where browsing may have masked the effects of burning. Conversely, 22 out of 125 undisturbed comparisons did show significant differences between treatments in height growth and number of leaves (although the height growth measurements are subject to the same limitations mentioned previously). The differences were between all treatments, indicating that the rate of recovery in raspberry is affected by burning to a greater degree than is hazel, and that the effects of different levels of fire disturbance are more evident in raspberry plants. Number of sprouts was not significantly different between treatments, indicating that, as in hazel,

burning reduces the rate of raspberry re-establishment but not the density of sprouts.

In general, the recovery rate data agree with other burning studies conducted in the boreal forest. Buckman (1964) burned hazel stands in northern Minnesota, and reported similar results. The above-ground portions of the plants were killed in his study, and profuse resprouting was recorded following a spring fire. He concluded that high duff moisture contents (102-117%) are sufficient to protect the underground reproductive organs of the hazel shrubs. He also burned stands of hazel in the summer under drier duff conditions (37-40% moisture content), and reported significantly fewer stems/acre following the fire.

6.3 Shrub Biomass

Shrub biomass measurements agree with the recovery rate data, especially in the case of hazel. The only significant difference was between the fuel-free plots and the fuel-added treatments. However, this result is subject to the same limitations described for the height growth measurements; that is the biomass on the fuel-free plots is comprised of that which was not consumed by the fire in addition to that produced following burning. Therefore, the biomass harvested was not entirely new growth.

The implications for wildlife management seem to be that in the first two growing seasons following burning,

total biomass is actually reduced on burned areas regardless of fire disturbance level. However, total biomass does not reflect the proportion of palatable new growth present; the higher biomass on the fuel-free plots may consist mostly of unpalatable woody stems. Therefore, even though the fuel-free plots had a higher total biomass, the utilizable browse may actually be higher on the burned plots.

The raspberry biomass measurements show no differences in mean biomass between any of the treatments. This result seems to confirm the results of the recovery rate data: raspberry is affected to a greater degree than hazel, i.e. post-fire influences have a greater impact on raspberry than on hazel plants. This may be due to the fact that raspberry stems and rhizomes occur relatively near the duff surface (Flinn and Wein 1977) and that they are smaller in diameter and succulent rather than woody. These conditions result in raspberry being more susceptible to disturbance by fire than hazel, and also more susceptible to post-fire disturbances.

6.4 Regenerative Mechanisms

The results of the greenhouse bioassay study indicate that under light to moderate burning conditions, buried seed and vegetative resprouting are equally important in post-fire plant re-establishment for plant species occurring in boreal aspen stands in Alberta. This result applies to the species observed as a whole; individual species may

reproduce using only one method or another. A few species seemed to be stimulated or inhibited by burning, but the majority were not appreciably affected. It should be mentioned that these results occurred under light to moderate burning conditions, and the response of these species to more severe burning may be very different.

Based on observations made in this study, the reproductive strategies of the target plants are quite different. Raspberry was equally represented by seed and vegetatively produced plants, and did not seem to be adversely affected by light burning. Raspberry was present in large numbers, and seems to reproduce readily following fire. These observations agree well with those made by others. Moore and Wein (1977) report that 90% of the viable seed recovered from undisturbed forest floor samples was Rubus strigosus, and several authors have reported profuse resprouting of raspberry following burning (Lutz 1956, Ahlgren 1960, Foote 1976).

The reproductive strategy of hazel is quite different from raspberry. No hazel seed was found in any of the duff cores, and all reproduction observed in the field was of vegetative origin. No sprouting was observed on the duff cores, and was probably due to the fact that the underground stems of hazel occur at the duff/soil interface (Hsiung 1951), and were not included in the duff cores. Hazel reproduces primarily from vegetative means following disturbance (Hsiung 1951), and reproduction from seed is

usually limited to sites that are undisturbed and possess a large population of small mammals (Tappeiner 1971).

6.5 Duff Depth/Weight Study

The regression relating duff depth to duff weight did not account for the variability found in the measurements. There are several reasons that may account for the high variability in the observations. First, a small amount of mineral soil was unavoidably included with each sample. Although the samples were oven-dried, clay in the mineral soil still contained structural water which is driven off at high temperatures. Differential thermal analysis for montmorillonite clay, the predominant clay on the study site, indicated that loss of structural water occurs at 600°C (MacKenzie 1964). The same analysis also indicated that bound water is driven off at 100-150°C. These water losses may account for some additional weight loss. However, the clay content of these soils is rather low (Crown 1977), and would probably not be sufficient to cause the degree of variability observed.

Another source of variability may be the different proportions of F and H layers in each sample. Each of these layers have different bulk densities, and since they represent different stages of decomposition, they may contain different relative amounts of ash and organic matter. Therefore, the amount of combustible material will

vary due to the different proportions of F and H layers present, as well as the depth of duff.

The proportion of F and H layers in the soil core may also vary due to differences in vegetative cover. The overstory vegetation on the site was relatively uniform, but the understory cover varied considerably between sample locations. Variation in understory composition will affect not only the amount of litter produced annually, but also the rate of decomposition. Differences in chemical makeup, palatability to micro-organisms, and resistance to weathering will all produce variations in rate of litter decomposition (Mellin 1930, Van Cleve 1971, MacLean and Wein 1978). Different rates of decomposition between sample locations would contribute to different proportions of F and H layers.

Local fire history may also have an effect on the proportion of different duff layers present. Forest fires are usually characterized by large variations in fire intensity (Van Wagner 1979), and seldom remove uniform amounts of duff. For example, a fire passing through the study site in the past may have removed a portion of the F layer, leaving the H layer unburned. An adjacent spot may have not been burned. Two adjacent samples would then have very different proportions of F and H layers present.

Mixing of mineral soil into the organic layers would also affect the results of the loss-on-ignition determination. Soil mixing in the park may be caused by soil

organisms, small burrowing mammals (Armson 1977), or buffalo rolling on the ground. Signs of past animal activity may not be evident, but could have contributed heavily to soil mixing.

In general, a duff weight/duff depth relationship seems to be a useful tool, in spite of the variability observed in this study. Previous attempts (McRae et al. 1979, Hawkes and Lawson 1980, Woodard and Martin 1980) have all produced significant relationships that enable site-specific determinations of duff weight from duff depth. Closer attention to sampling methodology would probably result in a more acceptable relationship for the boreal mixedwood forest as well.

6.6 Prescribed Burning in Aspen Stands

The fire behavior observed during the prescribed burn provided some insight into the advantages and problems associated with prescribed burning in aspen forests.

Early spring burning conditions seem to be ideal for fires of low to moderate severity in aspen stands in Alberta. The impact of fire on vegetation is minimized due to the high duff moisture content and the lack of green foliage (Bailey and Anderson 1980). Fuels consist mostly of light flashy grass and leaf litter with low residence times, and fires in these fuels are easily controlled with wet lines and narrow fuel breaks (Dube 1979). Spotting seldom

occurs because these small embers self-extinguish soon after being blown off the burn site. Crown fires are virtually non-existent in these stands due to the lack of dry foliage, short flame lengths, low crown bulk densities, and lack of ladder fuels (VanWagner 1977). Fires in these stands are generally limited to surface burning and present no major control problems.

Burning in late spring or early summer results in a different set of conditions. Once transpiration has begun, soil moisture on upland sites is rapidly depleted and the duff becomes dry enough to burn (Buckman 1964). Duff consumption may result in significant damage to underground reproductive organs (Flinn and Wein 1977) and to seed buried in the duff (Moore and Wein 1977).

Conversely, green foliage usually renders an aspen forest impossible to burn effectively; some workers have suggested using aspen stands as fire breaks (Fechner and Barrows 1976). Strong winds, low humidities, and high air temperatures are usually necessary to achieve adequate burning conditions in these stands, but they will also result in erratic and dangerous fire behavior (Wright and Bailey 1980). Dry dung piles, rotting logs, and deep duff accumulations may provide sites for holdover fires, and spot fires from rolling dung have been observed during prescribed burning in east-central Alberta (Bailey 1978). In addition, heavy accumulations of shrubby fuels often supply large numbers of firebrands which can cause extensive spotting

(Bailey and Anderson 1980).

Another approach to shrub eradication might be to burn these areas in the fall, following the first killing frost. The grass and leaf litter fuels will be dried, the absence of canopy foliage will prevent crown fires, and the shrub root reserves will be at their lowest levels. Buckman (1964) suggested that fall burning may result in substantial hazel mortality.

In general, spring burning conditions will produce surface fires of low to moderate severity, which are easily controlled. Summer burning usually requires more extreme weather conditions, resulting in erratic fires which are difficult to control.

7. Conclusions

1. Artificial fuelbeds provide an effective means of subjecting selected target plants to controlled levels of fire disturbance. Fuels can be fully documented as to moisture content, weight, and physical arrangement. Uniformity in fuelbed size and arrangement is easily achieved, and construction of the fuelbeds under field conditions presents no major difficulties. Burning conditions tend to be fairly uniform between similar fuelbeds, allowing replication of treatments. Fire behavior is easily documented, and can be varied over a range of disturbance levels. Burning treatments can be applied to individual plants, enabling observation of the specific effects of burning. Fire is easily confined to each fuelbed, reducing the need for a large suppression effort.
2. The most important fuels in aspen stands under spring burning conditions are grass and leaf litter. Woody fuels are not an important constituent of the fuel complex, and other vegetation is unlikely to burn because of high moisture contents and the lack of flammable foliage. Fuel loadings on the burn site averaged approximately 1 kg/m^2, and ranged from 0.5 to 4.0 kg/m^2.
3. Duff weight is poorly predicted from measurements of duff depth. Variability in observed duff weights, as determined by loss-on-ignition, may be explained by loss

of structural or bound water, variation in proportion of F and H layers, varying rates of understory foliage decomposition, and mixing of mineral and organic horizons through animal activity.

4. Weather conditions, fire weather indices, and fuel moisture contents were within previously published burning prescription limits, but were probably less than optimum. In spite of very dry spring weather, duff moisture remained high (121.3%).

5. Fire behavior under the aspen canopy was of low to moderate severity, and little damage to overstory trees resulted from burning. Fire intensities (I_B) measured in natural fuels varied from 50 to 18,600 kW/m. Fire intensity was highest in areas of heavy grass accumulation, but short residence times prevented damage to underground plant organs.

   Fire intensity has often been used in describing the severity of a fire and its impact on vegetation. However, the results of this study indicate that fire intensity, as expressed in kW/m or kW/m^2, may be inappropriate for measuring the impact of a fire on vegetation.

6. Two shrub species, beaked hazelnut (Corylus cornuta) and wild red raspberry (Rubus strigosus) were chosen to test the effects of varying levels of fire disturbance on post-fire plant re-establishment. Different levels of fire disturbance were achieved using excelsior and white

spruce slats packed around the base of each target plant. Total heat release was used to quantify the heat flux experienced by the target plants. Total heat release varied from 3217 to 180,439 kJ/m^2.

7. A solution of orthotolidine and hydrogen peroxide was used to determine the extent of fire-induced mortality on the two target species. All portions of above-ground stems exposed to heating were killed. There were no significant differences in amount of mortality between the various levels of fire disturbance. Below-ground mortality extended 1-3 cm below the duff surface on a few plots, but was not statistically significant. All other plots experienced no underground mortality. The lack of underground mortality was attributed to the high duff moisture content.
8. The recovery rates of the target plants were monitored following burning. The number of sprouts did not vary significantly between treatments. Height growth was significantly greater on the fuel-free plots, but this may have been due to poor measurement techniques. The number of leaves produced by each sprout differed significantly on only 41 of 250 comparisons. The lack of significant treatment effects was also attributed to the high duff moisture content.
9. The greenhouse bioassay study revealed that the number of species utilizing either buried seed or vegetative reproduction in post-fire plant re-establishment was

approximately equal. A few species seemed to be either stimulated or inhibited by burning, but most showed no effect. The duff cores were subjected to light burning only, and plant response at higher disturbance levels may be quite different. Average number of emerging plants did not vary significantly between burned and unburned cores, for either seed or vegetatively produced plants.

Susceptibility of hazel and raspberry to damage by fire varies because of their different reproductive strategies. Hazel did not reproduce from seed in the study area following disturbance, and its underground stems occur deeper than raspberry (5-10 cm below the duff surface). A severe fire would be required to damage underground hazel stems, and fires of this magnitude are unlikely to occur in aspen stands in the boreal forest. In addition, underground hazel stems are much larger in diameter than raspberry stems, and could probably withstand a greater amount of heating.

Raspberry seeds occur in the duff layer at depths as shallow as 2 cm. Observations made during this study indicate that raspberry rhizomes occur at depths of 0-5 cm, and are usually rather small in diameter (2-5 mm). Burning under conditions which allow substantial duff consumption would probably eliminate raspberry propagules from the site. In general, raspberry is more susceptible to fire than is hazel.

10. Prescribed burning under spring conditions in boreal mixedwood stands is unlikely to achieve the stated goals of the Elk Island National Park burning program. Use of burning to reduce or eliminate hazel encroachment will not be effective because of the regenerative mechanisms utilized by this species. Reproduction following fire occurs by resprouting from underground stems, and high spring duff moisture contents will prevent spring fires from damaging the reproductive organs. In addition, the lack of heavy fuel accumulations will reduce the fire disturbance level experienced by the shrubs, and short residence times of the grass and litter fuels are insufficient to provide adequate heat penetration.

    Summer prescribed burning under lower duff moisture conditions may result in some hazel mortality, but green foliage will prevent large-scale burns unless burning is conducted under hazardous conditions.

    However, if the objective of burning is to stimulate hazel sprouting, spring conditions are ideal. High duff moisture contents will prevent underground plant mortality, light flashy fuels will produce easily controlled fire behavior, and hazel will resprout profusely. Raspberry is also stimulated by moderate spring fires and will reproduce in large numbers.

8. Future Research

The results of this study indicate several future research needs. First, the role of the duff layer in protecting underground plant organs and as a potential fuel needs to be further investigated. Of particular importance is the effect of duff moisture content in protecting underground perennating buds. Duff moisture content should be followed through the growing season to determine the loss or increase of moisture as it is related to current weather conditions and vegetative phenology. In addition, duff moisture should be evaluated in different vegetation types to determine the differences and similarities between plant communities. Knowledge of the physical arrangement of the duff layer would assist in understanding the role of duff as a fuel. Bulk density of the L, F and H layers, the effect of leaf arrangement and size on moisture relations, and the variation in the proportions of the L, F and H layers all remain to be investigated. The heats of combustion of the various duff layers have not been determined, and would allow the quantification of heat output during duff combustion.

In addition to the duff layers, the role of other fuels in boreal mixedwood stands should be further investigated. Rates of grass and litter accumulation should be determined, and more efficient methods of measuring these fuels need to be developed. Currently used line intercept methods of fuel inventory (McRae et al. 1979) are appropriate for woody

fuels, but are not applicable for herbaceous fuels. The importance of shrub fuels is currently unknown, and information concerning their weight and physical arrangement would be beneficial. More refined methods of estimating duff fuels should also be developed. The attempt made during this study to predict duff loading from duff depth measurements indicates that this approach has value. Subsequent efforts should include a larger sample size, and samples should be taken from a number of mixedwood stands. In general, the fuel complex in mixedwood stands has received little attention, and further information about fire/fuel relationships would contribute to better utilization of prescribed fire as a management tool in the boreal forest.

Prescribed burning should be attempted over a range of fuel, weather, and grazing conditions to determine the most suitable time for burning. Burning under various fuel conditions (cured vs. green) and in different seasons (spring, summer, fall) would indicate the optimum time for burning and would also indicate whether burning is feasible under marginal conditions. Current burning prescriptions are based on little practical experience, and actual burning would indicate potential problems and give personnel on-the-ground training. In addition, burning under different duff moisture conditions is very important because of the large effect duff moisture has on plant response to fire. Burning prescriptions could be written to stimulate browse production (high duff moisture) or for maximum shrub

mortality (low duff moisture). Burning should also be carried out in areas outside of the park where animal influences would be different.

Burning in other plant communities in the park should be undertaken in pursuit of other management goals. If duplication of historic fire frequencies is desired in grass or spruce communities, experimental burning in these communities needs to be carried out to determine the appropriate season and optimum burning conditions. Similarly, other uses of prescribed burning (e.g. hazard reduction, vegetation manipulation, wildlife habitat improvement) should not be implemented until specific burning prescriptions have been developed. A comprehensive prescribed burning program should include detailed pre- and post-burn documentation of fuels and plant communities.

Repeated burning in the same plant community should be carried out to assess the effect on undesirable plant species. In areas where eradication is desired, repeated burning may result in sufficient mortality. Preliminary work performed by Dube (pers. comm.)[7] in the park indicates that repeated burning in hazel communities may result in substantial mortality. This may be an effective approach in limiting shrub encroachment onto valuable grazing areas.

The clonal nature of some shrubs (especially hazel) should be further investigated as it relates to recovery

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[7] D. Dube, Fire Ecologist. Canadian Forestry Service, Edmonton, Alberta. Personal communication, 1980.

from fire. Burned plants may receive additional nutrients from adjoining plants to which they are attached underground. The extent to which this occurs is currently unknown, and may have a very large influence on post-fire plant re-establishment.

The effect of burning on browse production has not been investigated for the Elk Island National Park area. Due to the importance of wildlife management in the area, burning should be intensively evaluated as a habitat management tool. These studies should be integrated with others, including ungulate population dynamics, to determine the overall interactions between fire and wildlife.

A rather unique aspect of the park is the distribution of white spruce. This species is currently limited to lake shores and some islands in Astotin Lake, presumably due to the large fire in 1895 (Kjorlien 1977). A detailed investigation of the distribution and reproduction of white spruce would indicate the fire history of these spruce stands and the potential for future spruce establishment in other areas of the park.

Finally, the cause of the secondary disturbance observed in this study should be investigated. Possible causes for negative height growth included browsing, soil subsidence, insect herbivory, physiological changes in the plant, and others. However, none of these agents were actually observed, and the real cause is still unknown. The impact of this disturbance on plant growth was substantial,

and its cause should be determined.

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APPENDIX I. Quantities and Equations used in Fuelbed and Fire Intensity Measurements.

Quantities		Source
Particle density of white spruce (ρp)	432.5 kg/m³	Pashin and de Zeeuw (1980)
Heat of combustion of white spruce (H)	18,600 kJ/kg	Byram (1959)
Surface area/volume ratio (σ)	43.5 cm^{-1}	Brown (1970)

Equations

Fuelbed bulk density	$(\rho b) = \frac{Wo}{\delta} \times 100$	Wilson (1980)
Packing ratio (β)	$(\beta) = \frac{\rho b}{\rho p}$	Wilson (1980)
Fireline (Byram's) intensity (I_B)	$I_B = Hwr$	Byram (1959)
Reaction intensity (I_R)	$I_R = - \frac{dw}{dt} H$	Rothermel (1972)
Flame length (F_L)	$F_L = 0.0722\ I_B^{0.46}$	Wilson (1980)
Crown scorch height (h_s)	$h_s = 0.1483\ I_B^{0.667}$	VanWagner (1973)

Input Parameters

Wo = ovendry fuel loading (kg/m²)
w = ovendry fuel consumed (kg/m²)
δ = fuelbed depth (cm)
ρb = fuelbed bulk density (kg/m³)
ρp = particle density (kg/m³)
I_B = fireline (Byrams) intensity (kW/m)
I_R = reaction intensity (kW/m²)
H = heat of combustion (kJ/kg)
r = rate of spread (m/min)
F_L = flame length (meters)
h_s = height of crown scorch (meters)